ENDEAVOUR

A quarterly review designed to record the progress of the sciences in the service of mankind

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The future of man

The deliberate release of atomic energy comes as the climax of two centuries of science. It may well prove to be the most momentous event in the history of mankind. There are many men, and they not the least wise, who see no hope for the human race except by calling a complete halt to scientific research. Their imagination, fed by the appalling horrors of the last few years, pictures only too vividly the universal catastrophe likely to follow the use of the new source of energy for purposes of warfare. That the possibility of such catastrophe exists it would be idle to deny; but the suggested remedy is neither practicable nor desirable. It is inherent in the nature of man that he should seek new realms for exploration, both in thought and in action, and no legislation could stifle the urge. On the other count, it must be recognized that scientific knowledge has at least as great potentialities for good as for evil, and that to cut off science would be to cut off the main hope of human betterment. What is happening in the present phase of history is that science is creating problems at a rate greater than that at which they can be solved; but it is a counsel of despair to assume that such disparity will not in time be adjusted.

In considering the world-problems of today it is easy to lose sight of the fact that man is a product of organic evolution, and that evolution is a dynamic process still in operation. Any attempt to descry beyond the immediate future must therefore reckon with the possibility of further evolutionary changes, and from such a standpoint we may be able to form a sounder judgment of current difficulties. In the present issue we publish an article by Dr Julian Huxley on the subject of evolution. One of the most interesting conclusions that he reaches concerns man himself. Morphologically, man has changed comparatively little since the date of the earliest known human remains. He has not, as it were, spent his evolutionary capital in branching out into highly specialized new forms. In all other important types of organism this kind of specialization has ultimately come to a standstill, further changes resulting only in the formation of new species and genera and not in completely new types. It therefore seems possible that in man, whose history as measured in geological units is still very brief, such changes are yet to come.

Man differs from all other organisms in possessing highly-developed reasoning powers which allow him considerable control over his environment. As a result, purely morphological changes are unlikely to have much effect upon his history —to fly it is not necessary for him to grow wings, and he can cross the seas without swimming. *Per contra*, inasmuch as he depends more and more upon his intellectual endowment any evolutionary changes in this respect might be of fundamental significance.

It is difficult to arrive at any estimate of the probability of these changes. From written records and from investigations of early civilizations the conclusion seems inescapable that, during the last five or six thousand years, the human mind has not appreciably improved in ability. The sages of ancient Egypt, Assyria, and Babylonia, the philosophers of classical antiquity, and the intelligentsia of India, China, and Islam appear to have been as capable of intensive and fruitful thought as their best modern counterparts. True, their thought was directed in different directions from those we tend to follow today; but there is no reason to suppose that, had they had at their disposal our tradition and store of knowledge, men of two or three thousand years ago could not have made the discoveries that are at once the glory and the peril of the twentieth century. The reasoning power was certainly there, but the pabulum for its exercise and

nourishment had not yet been accumulated. That the average man of 1946 is very much better informed than his predecessors of even a century ago must surely be ascribed to better methods for the dissemination of knowledge rather than to an increased power of assimilating it. And it can hardly be disputed that one of the chief reasons for our present troubles is this wide extension of knowledge to people whose minds are not sufficiently cultured to make proper use of it.

It therefore seems likely that, while the possibility of a sudden evolution of man's mental capacity and quality cannot be altogether ruled out, the chances are that he will continue to make discoveries—and use or misuse them—with very much the same level of intelligence as he possesses today. There is, however, another possible factor to be considered. Hitherto there has been no sign that the progress of science is being hindered by the limitations of the human brain, but we may legitimately surmise that sooner or later a stage will be reached when the mind is inadequate to effect further advance. The continued existence of warfare may perhaps be taken as an indication that this stage has indeed already been arrived at, so far as morals and ethics are concerned; its eventual attainment in the quest for scientific knowledge would then be equally sure.

These reflections lead us to the interesting speculation whether it may in the future be possible to improve the human brain artificially. Events of the last few years, in all branches of science, demonstrate that such a speculation is not to be ranked as wildly fantastic: the scientist's dream of yesterday has recently been in the habit of coming true today. Substances—such as amphetamine—are already known which, on the basis of simple intelligence tests, appear temporarily to increase the power of reasoning, while the intellectual stimulation afforded by cocaine has long been a commonplace in the sensational novel. All drugs of this kind hitherto discovered suffer from serious disadvantages which would preclude their general use even were their mental effects of substantial value; but it is by no means unlikely that coming generations of biochemists may synthesize substances in which the beneficial reactions are enhanced and the deleterious reduced to a negligible minimum.

Chemical stimulation is of course only one of several ways in which it is conceivable that the capacity of the human brain may be better equipped for the tasks it will be required to undertake. Recent progress in experimental biology suggests that chromosome control may be a powerful tool in shaping the forms of life, and in due course it might prove applicable to man himself. In any case, whenever and however it is brought about, we have every reason for believing that man will be able to improve upon natural man, for such an achievement would be no more of a miracle than much that he has already accomplished.

The doubt remains whether science has so far outstripped the development of moral character as to render the years immediately ahead the most critical and dangerous period in the history of the world. That there should be a variety of opinions on this point is not surprising. The shocking devastation caused by the two atomic bombs dropped over Japan raises hopes in some minds that all nations will in future abstain from war, if only because victor and vanquished would probably be engulfed in a common ruin. Others, with a fatalistic bias, are pessimistic about the common sense of man, and foresee the suicide of civilization and indeed of man, with the instrument that represents his supreme effort of logical thought. Only time will show which of these two schools is correct—if either; but it is perhaps unduly gloomy to suppose that, even in an atomic war, the survivors would be so few that the human race would be completely unable to resuscitate civilized life. Many great civilizations of the past were destroyed or sank into decay, but these events, grievous and calamitous as they must have been at the time, have not prevented the more or less steady development of mankind as a whole. If the growth of civilization is an evolutionary process, we should remember when considering it that evolution is no longer regarded as continuous but rather as arising from many different points and proceeding along several paths, sometimes divergent, sometimes convergent. The world may now be standing at one of the junctions.

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Species and evolution

JULIAN S. HUXLEY

Less than a century has elapsed since Charles Darwin enunciated the evidence for organic evolution in his celebrated *Origin of Species*. Today the fundamental truth of the theory is firmly established, and biologists are no longer concerned with proof of the reality of evolution; the problem is to elucidate its mechanism. In this article Dr Huxley discusses current views on the subject. He reaches the interesting conclusion that, except in the case of man himself, the most important evolutionary changes have probably run their course.

THE PROBLEM AND ITS EXTENT

When Darwin wrote his great work, he called it the *Origin of Species* because that was then the crux of evolution. Either species were fixed and permanent in their characters, as they had been created in the beginning 'each after their kind,' in which case evolution was ruled out; or they could change into quite different types, in which case evolution must be accepted.

Today the position is entirely different. Evolution is generally accepted as a fact; we know that species change. Biologists are now trying to discover what they can about the different modes of evolution, the different kinds of species, and the different ways in which they may originate.

A main distinction which has emerged is between long-term trends on the one hand, leading usually to an improvement of general type, and short-term diversification on the other. The difference between the two can be illustrated from any modern mammalian type. The horse stock, for instance, showed a steady increase in efficiency of hoofs and of grinding teeth throughout tens of millions of years. That was a long-term trend. But today the horse, the zebras, and the asses merely ring minor changes on the general perfected equine plan (figure 1), and in every epoch the type was diversified into many different species, all at approximately the same level of the main trend.

What is a species? In one sense it is just a group of similar animals or plants which it has been agreed to distinguish by means of a Latin name. Thus the birds popularly called Lesser Redpolls are assigned to the species *Carduelis flammea*, *Carduelis* being the name of the genus, *flammea* of one of the species within it. But this assigning of specific names is not merely arbitrary. Species are also natural groups, which can usually be defined by a combination of the following criteria. First, their members inhabit a geographical area which is in accord with the idea of a single common origin for the whole. Secondly, they either interbreed, or are potentially capable of interbreeding, with each other. Thirdly, they possess certain distinctive common characters. Fourthly, they usually do not interbreed with other specific groups, or, if they do so, fertility is reduced.

There are exceptions to all these criteria; they have different weight in different forms; and there are borderline cases where evolution has taken a group half-way to specific distinctness. We must expect a compromise between the human need for pigeon-holing facts and the variety and fluidity of nature. Yet in well-worked groups there is remarkable agreement as to what should be called species. Thus in birds, Ernst Mayr estimates that fewer than 1 per cent. of the thousands of named species are doubtful or disputable.

The extent of the species problem can be realized when we discover that something like a million species of animals have already been named, and that new discovery is still adding to the list, and at an increasing, not a decreasing, rate.

However, more interesting than semi-philosophical disputes about definitions are the investigations which are showing how groups actually vary in nature and how biological discontinuities arise in them, and may be accentuated.[1]

Let us first look at diversification within species. I spoke earlier of the Lesser Redpoll. This breeds in Britain and much of central Europe. In northern Europe, and also in Siberia and Canada, the breeding redpolls, though very similar, are definitely paler and a little bigger: their popular name is Mealy Redpoll. In Greenland they are still larger, but not so pale as the Mealy. These three geographical groups are too alike to be called species; they are therefore called *subspecies*,

[1] The species problem is still fluid. A brief essay such as this inevitably fails to do justice to the complexity of nature, or to take account of various points of view held by other biologists.

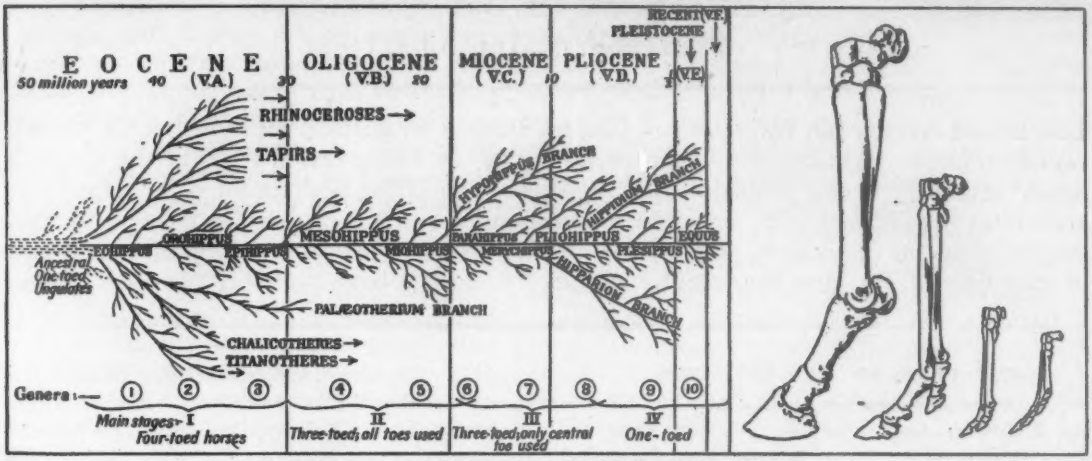


FIGURE 1 – *A long-term trend. The evolution of horses.*

(a) left. The horse stock took something like fifty million years to evolve from the original odd-toed ungulates. (The time-scale of the Pleistocene and recent periods is magnified relative to the rest of the diagram.) Numerous side branches were produced and became extinct, but the main trend was continuous.

(b) right. Stages in the trend: a series of left fore-feet. Right, Eohippus with three of its four toes visible (fifth, fourth, and third). Next, Mesohippus with three longer toes, all used. The fifth digit is reduced to a small splint bone. Next, Merychippus. It possesses hoofs, but the fourth and second digits are small and lifted off the ground, the third (central) digit is enlarged. Left, a modern horse (Equus). The second and fourth digits are reduced to splints and have lost their hoofs. The central digit is much enlarged and has a big hoof. The general trend is towards greater size and rapid running.

(From The Science of Life, *3-volume edition. By permission of H. G. Wells, J. S. Huxley, and G. P. Wells.*)

and given a third name—the Lesser Redpoll is *Carduelis flammea cabaret;* the Mealy is *C. f. flammea;* and the Greenland is *C. f. rostrata* (figure 3). Another set of high northern redpolls is quite definitely distinct, in having an unstriped white rump and belly. It is therefore assigned to a different species, *C. hornemanni.*

GEOGRAPHICAL SUBSPECIES

Distinct forms on islands cannot interbreed freely with their neighbours; but when they are so similar that they can be presumed to be capable of fertile crossing, they also are called subspecies. Thus in Britain, the wrens on St. Kilda are uniformly larger, heavier-billed, and with more barring than those of the mainland.

In the diversification of species by geography, several different factors are at work. There is on the one hand adaptation to local conditions; on the other there is the effect of isolation, which allows much more rapid divergence of groups; and there is the size of the group—in isolated small populations non-adaptive 'accidental' changes may become established.

With regard to the species of North American Deermouse, *Peromyscus polionotus,* Sumner has given us some very interesting facts from Florida (figure 4). On an isolated reef of white sand, a distinct, almost white, subspecies is found. The coastal strip, about 35 miles wide, has lightish sandy soil and is inhabited by a moderately pale subspecies. The inland area has heavy dark soil, with a dark subspecies, its colour nicely adapted to that of the soil. The white form is a protective adaptation to the white sand. But its origin has been made possible by breeding isolation; for on the equally white beach of the mainland shore, the mice are merely rather paler than further inland.

Where the pale and dark mainland subspecies meet, there is a belt, only a few miles wide, where the average colour changes very rapidly from pale to dark. But besides this change in average, there is to be noted a sharp increase in variability. This can only mean that two distinct types here interbreed, with resultant recombination of characters. There is clearly a general adaptation of both the subspecies to soil colour. In addition, it seems that each is 'internally adapted,' through the development of its own distinctive complex of genes, or hereditary units, making for vigour, fertility, and so on. When two such gene-complexes are crossed, most of the recombinations will be less well-adjusted, and their spread will be discouraged by natural selection; this will keep the hybrid zone narrow.

There are two complications. The coastal form seems to have expanded recently on to the edge of the dark inland soil, along the seaward side of which there is a narrow belt of white sand. Thus so far as colour goes, selection will be making the coastal form paler on one margin, darker on the other, and a gradient of characters (or 'cline' as it has been called) is the result.

Quite a number of birds and mammals show this general feature of stabilized subspecies remaining fairly constant over comparatively large regions, and being separated by narrow belts in which the character changes rapidly.

There are other cases where the inhabitants of a continuous area differ in different parts of it sufficiently to warrant being called subspecies, but no sharp steps, no narrow intergrading zones, have been found. This may sometimes be due to insufficiency of facts—as more specimens accumulate and the steps are looked for, they will turn out to be there after all. But nature is almost perversely varied, and sometimes continuous slight variation seems to operate over very large stretches. This is true for the sharp-tailed grouse over the great plains of North America.

ECOTYPES

In regard to plants, botanists generally prefer to use the word *ecotype* to denote the lower units of which species are made up. The primary meaning is a form or group adapted to a particular set of environmental conditions. It was the Swedish botanist Turesson who first gave currency to the term. For instance, in the grass *Poa alpina* in Scandinavia, he showed that there were three distinguishable ecotypes, from alpine, subalpine, and lowland habitats. These differ in various visible ways, but also in more important ecological characters, such as water-requirement and time of flowering. The basic differences are hereditary.

Sometimes the ecotypes are just like subspecies in higher animals. Thus a team of Californian botanists, under the leadership of Clausen, has been growing ecotypes of various plant species at experimental stations at various heights. To take one example, the potentilla, *P. glandulosa*, has a well-marked climatic ecotype in the Coast Range, and another in the Sierra Nevada foothills. The two are separated geographically and are obvious subspecies. When we get higher up in the Sierra, however, things become rather different. After a certain altitude a hill-meadow ecotype overlaps with the foothill form. However, even in the overlap zone the two are kept separate by their ecological requirements: the foothill form is practically restricted to the dry hillsides, the higher one to moist meadows.

Gregor in Scotland has described an extension of this kind of arrangement in the common sea-plantain, *Plantago maritima*. In many areas, there is a steady gradation from waterlogged, salty mud to dry, less maritime conditions. The plantains then also show a corresponding gradation in various characters—average height, for example, ranging from about 20 cm. to nearly 50 cm. The evidence goes to show that the environment seems to act as a sieve. A great range of different ecotypes must be produced, but they are sifted out by their requirements, so that even a rapid gradation in the environment is reflected in a gradation in the plant's characters: ecotype here is therefore quite different from subspecies.

To return to the Californian potentilla, it was found that, at still greater heights, there were a subalpine and an alpine ecotype. The one was taller and later-flowering, the other definitely dwarfish and early-flowering. But in this case the two ecotypes grade gradually into each other over a belt of considerable width.

These examples will show some of the complexities of the picture. Very broadly, we may say that the species of higher animals tend to be divisible into geographical sub-groups, those of higher plants into ecological or habitat sub-groups, though there are exceptions, and though broad ecological adaptation will often coincide with geographical separation. The difference, so far as it is real, is presumably related to the more random methods of fertilization and of dispersal in the plants, which facilitate sifting by habitat.

GEOGRAPHICAL ISOLATION

It is when isolation is at work that the divergence of groups can, and often does, become accentuated. This is true both for the formation of subspecies and for full species. In addition, small populations, as Professor Sewall Wright has shown, are liable to what we may call evolutionary accident. In them, many old genes may die out entirely, and useless (or even deleterious) mutations or gene-combinations may become fixed, owing to mere chance.

A pretty example of this comes from lizards on the Adriatic. Sinking of the coast has isolated lizard populations on a number of islands. As we might expect, the degree of difference of the island populations from the mainland form increases roughly with the time they have been

separated (as measured by the depth of water between island and mainland). But it also does so with decrease in the size of the island, and therefore of the size of the population.

Similarly, Dr Uvarov tells me that quite small groups of flightless grasshoppers which occur in isolated patches in arid regions may be sharply distinct from each other.

Quite apart from the size of population, isolation encourages diversification. An excellent example is the little Malayan Mouse-deer. This is represented by a single subspecies of uniform type over the whole of Sumatra and Borneo; but on the islands of the Rhio Linga archipelago, with less than 1/150th of the area, no fewer than seven distinct subspecies have evolved.

Not merely subspecies but obviously full species may develop through isolation. Thus in Britain, our red grouse is clearly derived from the same stock as the willow grouse of continental Europe. Yet it differs not merely in such minor features as its dark wing-feathers, but in not changing colour to white in winter. It is accordingly ranked as a distinct species, with the name *Lagopus scoticus*. It is interesting that no other British bird has reached more than subspecific difference.

This seems to be due to lack of time, for, on old archipelagoes, the process may go further. Mayr illustrates this from the Barking Pigeons (*Ducula*) in the Pacific (figure 2).

Once isolation has allowed the evolution of distinct forms which will not interbreed, these species may spread out and come to overlap in their distribution, instead of replacing each other in different geographical areas like mere subspecies. The two forms generally differ somewhat in adaptation and way of life. Thus our closely related willow-warbler and chiffchaff now live side by side in Britain, but are adapted to somewhat different habitats. There has been a real diversification of the original leaf-warbler type—though where the original separation occurred we do not know.

LARGE-SCALE DIVERSIFICATION

When combined isolation and diversification continue for long periods, we can sometimes see genera and families being evolved. A single group may radiate out in many directions, which are often adaptive, though more or less accidental differences also occur. The classical case of this is provided by the groundfinches of the Galapagos archipelago. They are classical because they were one of the chief reasons which forced Darwin to believe in evolution.

The Galapagos archipelago comprises some nine larger and a number of smaller volcanic islands. The nearest mainland is the west coast of South America, over 600 miles distant. The groundfinches (*Geospizidae*) are a distinct family, confined to the archipelago (and to Cocos Island):

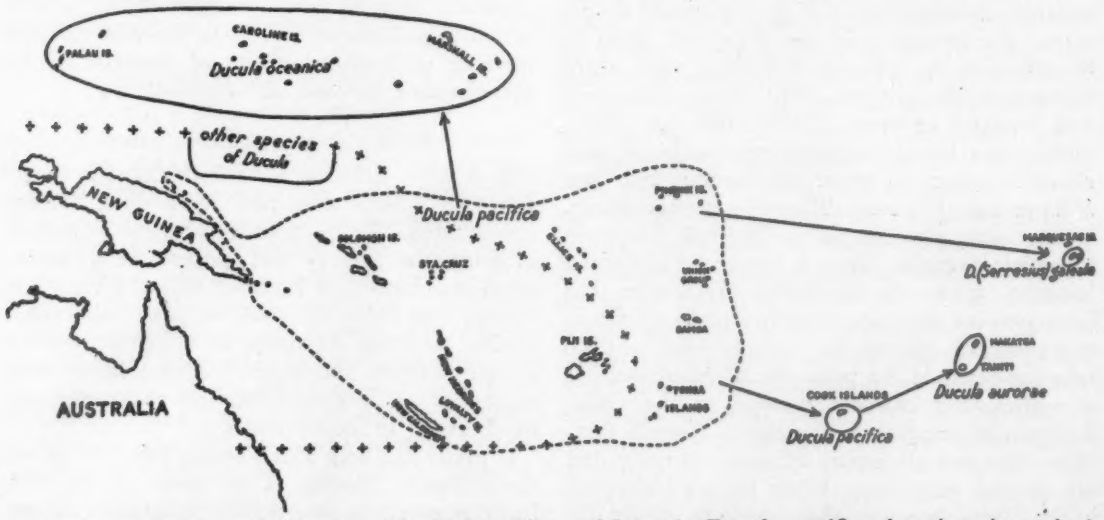
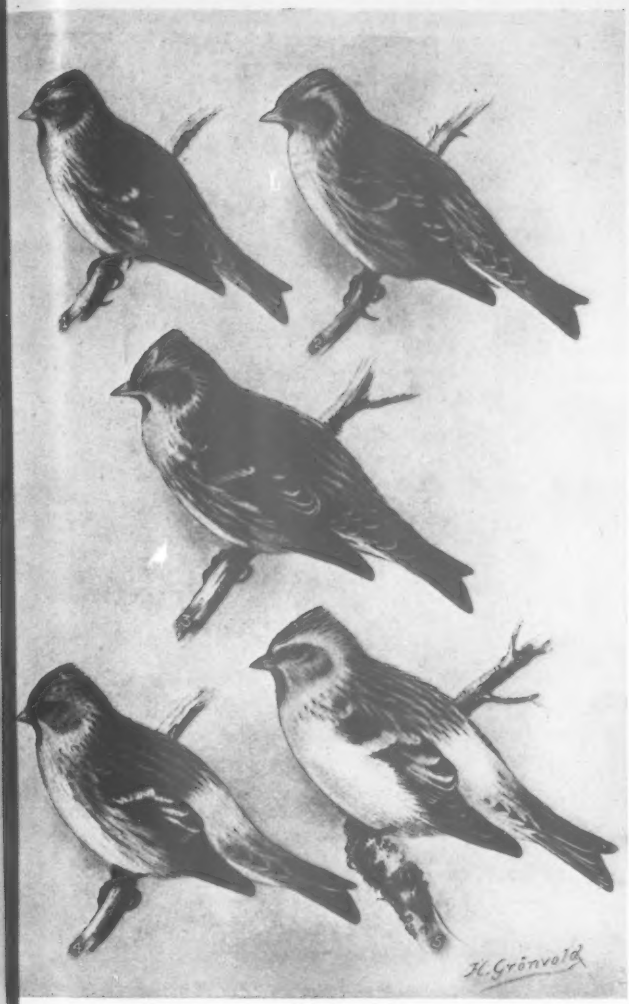
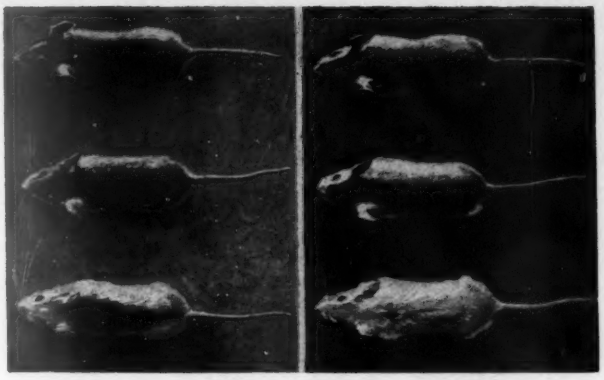


FIGURE 2 – *Isolation and divergence. The Barking Pigeon of Polynesia,* Ducula pacifica, *has given rise to closely related species to the north and on Tahiti. On the isolated Marquesas Islands it has produced a species so different in beak-shape that it was originally classified in a different genus.*

(From E. Mayr, Systematics and the Origin of Species. *By courtesy of Columbia University Press.)*



URE 3 – *Species and geographical subspecies of redpoll* (*see text*).
to (3) Carduelis flammea. (1) *Lesser Redpoll*, (2) *Mealy Redpoll*,
Greenland Redpoll.
and (5) Carduelis hornemanni. *Subspecies from Greenland, and from*
land and North Russia.
H. F. Witherby, et al., Handbook of British Birds. *By courtesy of Messrs. H. F. & G. Witherby.*)



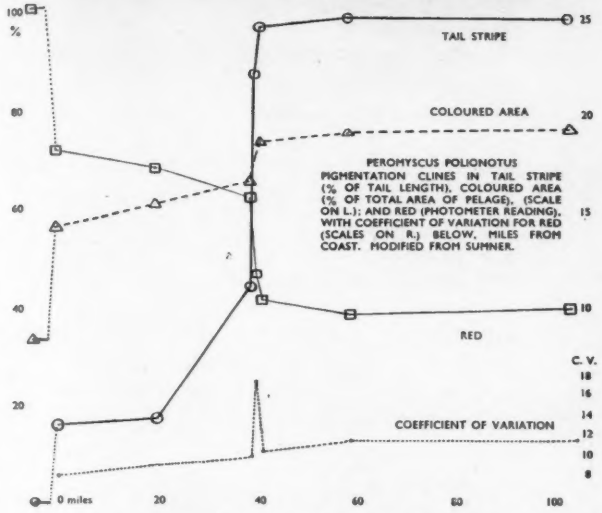


FIGURE 4 – *Subspecies in an American Deermouse* (*see text*).
(*a*) *top. The inland, coastal, and island subspecies. On the left, against a background of white sand, on which the island form lives; on the right, against the dark soil from the area of the inland form.*

(*b*) *The accompanying graph shows the effect of selection and isolation on pigmentation. The island subspecies* (*left-hand point*) *is isolated. The coastal subspecies grows darker until the zone of admixture and increased variability is reached* (40 *miles from the coast*). *The inland subspecies is almost uniform.* (*The amount of red decreases with increasingly dark colour.*)

(*a*) *From* The Science of Life (*3-volume edition*). *By permission of H. G. Wells, J. S. Huxley, and G. P. Wells.*
(*b*) *After J. S. Huxley in* Bijdragen tot de Dierkunde (*Leiden*), 1939.

FIGURE 5 (*left*) – *The synthesis of a species.* (1) *and* (3) Galeopsis speciosa *and* G. pubescens, *two wild labiates, each with* ($n = 8$) *chromosomes. The hybrid between them was almost sterile, but eventually doubled the number of its chromosomes, and became fertile. This new fertile tetraploid species is practically indistinguishable from another wild species,* G. tetrahit.
(*From A. Müntzing*, Hereditas (*Lund, Sweden*), *Vol.* 14. *By courtesy of the author and publisher.*)

FIGURE 6 – *Borderline species.*

(a) top. The Carrion and Hoodie crows are very distinct in colouration.

(b) left. But where they have re-met after the ice-age they interbreed and give fertile hybrids. The range of the Carrion crow is indicated by dots, that of the Hoodie by vertical lines, and the belts of interbreeding by dark shading (see text).

(a) From Yarrell's British Birds. *(b) From H. F. Witherby,* et al., Handbook of British Birds. *By courtesy of Messrs. H. F. and G. Witherby.*

FIGURE 7 – *An allotetraploid species may be more successful than its parents.* Spartina townsendii *(see text) has been able to colonize areas over which the indigenous parent species* S. stricta *was unable to spread.*

(a) left. Early stages in the colonization of bare mud in Poole Harbour. *(Photograph by R. V. Sherring.)*

(b) right. Approximately the same view, thirteen years later. *(Photograph by F. W. Oliver.)*

(From A. G. Tansley, The British Islands and their Vegetation. *By permission of the author.)*

they do not occur on the mainland. The entire family must have arisen from a single pair of some kind of finch accidentally blown out to sea. They have since evolved into five well-marked genera, with nearly 20 species (figure 8).

Even greater diversification has taken place among the sicklebill family (*Drepanididae*), confined to the Hawaiian archipelago (and Laysan Island). They have evolved into 18 distinct genera (with some 40 species), including not merely seed-eaters and insect-eaters, but nectar-suckers with special tongues, and a unique 'woodpecker' type (*Heterorhynchus*) which has a long upper mandible adapted to pry away bark, and a short lower mandible for pecking out grubs in the wood. Some authorities consider that they show diversification in more adaptive directions than any other family of birds.

On oceanic archipelagoes, there seems to be another factor at work besides isolation: since the fauna is a very restricted one, being confined to the descendants of comparatively few accidental stragglers, there is less competition. This biological low pressure makes it easier for new adaptive specializations to arise. If there had already been woodpeckers in Hawaii, we can be pretty sure that the woodpecking adaptations of *Heterorhynchus* would not have been evolved.

Something similar appears to happen when enemies are fewer: low predator-pressure may act in the same sort of way as low competition-pressure. The best example of this comes from the little Cichlid fish of the East African lakes. All these lakes are isolated, and in each there are Cichlid species peculiar to that lake, or *endemics* as the biologist calls them. The big predaceous fish *Lates* and *Hydrocyon* have managed to invade some of these lakes, but not others. Where they are absent and predator-pressure is low, many more endemic species, adapted to more ways of life, have evolved. Apparently new evolutionary ventures do not get the same chance of survival when opposed by the streamlining pressure of powerful enemies.

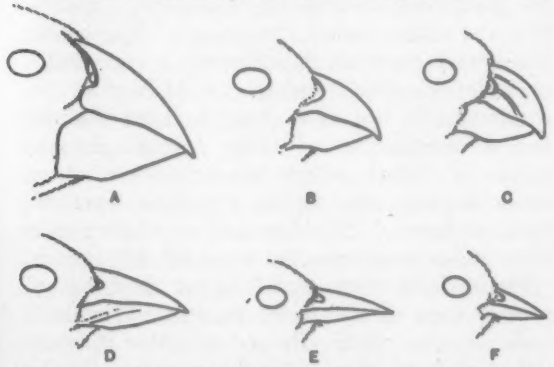


FIGURE 8 – *Divergent radiation in the groundfinches. On the Galapagos archipelago five different genera have been evolved.* (A) Geospiza, *includes large-billed seed-eaters.* (B) Platyspiza, *mainly leaf-eating.* (C) Camarhynchus, *mainly insectivorous.* (D) Cactospiza, *uses a twig to pry insects out of wood.* (E) *Is a similar slender-billed form from Cocos Island.* (F) Certhidea, *warbler-like.*

(*After H. S. Swarth. By courtesy of* Biological Reviews, *Cambridge.*)

ECOLOGICAL ISOLATION

If such numerous and diverse types have arisen in a continuous body of water, we must suppose that in animals geographical isolation is not the only avenue to achievement of the rank of full species, and that isolation by habit or habitat is also possible. It is difficult to visualize the process, and some authorities refuse to admit it. However, there are certain cases where it seems definitely established. Thus among insects restricted to one or a few food-plants, we may find so-called 'biological races' with different food-preferences. For example, the ermine moth has one race adapted to apples, the other to hawthorn and blackthorn. The apple form usually starts its larval life as a leaf-miner, the other not. Given a choice of food-plants the larvae of both races show an 80 to 90 per cent. preference for their own; and an almost equally high fixation is shown by the female moths in their egg-laying preferences. Caterpillars forced to eat the 'wrong' food give moths which are generally undersized and often infertile. Finally, the mating-preference between males and females of the same race is twice as strong as that between those of different race. Thus, though the two races may coexist in the same area, they are halfway to separation as distinct species. In other insects, this type of divergence has produced full species.

We know that many pests of cultivated plants have arisen through a change in food-preference. For instance a bug, *Plesicoris rugicollis*, which in nature is confined to willows, in 1918 began turning its attention to apples, and later the apple race became quite a pest.

How a species gets on to a new food-plant, we do not know. But once a new source of food has been successfully colonized, there is some ecological isolation, and the new strain may persist and evolve. For the adults which emerge are 'conditioned,' in the psychologists' phrase, to the smell of the plant they have fed on as larvae, and will often prefer it to the original species. Thorpe

has made experiments in flavouring the food of fruit-fly grubs with different chemicals and finds that, even in this more mixed feeder, a considerable conditioning of the adults' egg-laying preferences takes place.

Thorpe's results are a beautiful experimental confirmation of the principle of 'Organic Selection' put forward long ago by Baldwin and by Lloyd Morgan. They suggested that a change of habits, without any inherited alteration, might often be the first step in evolution. The strain would be held, more or less firmly, by its habits in a new niche, until such time as mutation and selection could provide a hereditary constitution adapted to the new environment.

CLOSE SPECIES

Sometimes when closely related species occupy the same area, the mating barriers between them seem to have been intensified by natural selection. Thus our familiar chiffchaff and willow-warbler are extremely alike in most ways, but differ strikingly in their song (occasionally the chiffchaff will add a warble to its unwarblerlike two notes, indicating that these are a recent acquisition).

Often, however, no such obvious distinctions arise, and only painstaking research will show that what was at one time regarded as a single species is in reality two or more. Thus it was once believed that there existed one species of malaria mosquito in Europe—*Anopheles maculipennis*. Now it turns out that there are at least five or six reproductively isolated groups, i.e. species. These differ hardly or not at all in the adult, and very slightly in the larvae, but can all be distinguished by their egg-floats—in shape, colour, and pattern. They also differ in their habits, in the degree of their tolerance of salt-water, and in their capacity to transmit malaria to man.

Sometimes we can understand just how these almost identical species have come into being. The little brown tree-creepers of Europe really belong to two distinct species. The western, our *Certhia familiaris*, has a rather shorter beak and a longer and less bent hind-claw, and is slightly lighter-coloured than the eastern *C. brachydactyla*. They overlap over a broad zone in central Europe, but seem never to interbreed. Their distinctness was discovered by C. L. Brehm over a hundred years ago; but most ornithologists refused for some seventy years to believe that two creatures so alike could really be distinct species.

The explanation seems to be as follows. In the glacial period the spread of the ice split the range of the original single creeper species in two. A south-western and a south-eastern group were isolated. In their isolation they became just different enough not to cross. So when the ice finally receded they did not merely spread back again but could overlap without losing their separateness.

Perhaps even more striking are the chains of subspecies which are continuous, yet whose terminal links will not breed with each other (see figure 9). The entire group is one and two species simultaneously—or, if you prefer it, two of its subspecies behave as species when they meet.

When groups re-meet after separation, their divergence may not have proceeded all the way to wards full separation, and they will still interbreed. The crows provide an example from our own islands. During the ice age the eastern European group must have evolved the striking pied grey-and-black plumage of the Hoodie, while the Carrion crow of the south-western area stayed black.[1] The two forms have now re-met, and where they meet form a narrow band of hybrids of every type (figure 6). In Europe the interbreeding zone runs south of the Alps and up to the western Baltic.

CROSSING AND CHROMOSOME-DOUBLING IN PLANTS

In plants, matters are more complicated, for what are undoubtedly quite separate species will not infrequently hybridize easily and give fertile offspring. Thus the purple-flowered lucerne (*Medicago sativa*) imported into Europe as a forage plant in the seventeenth century, seems speedily to have crossed with the indigenous yellow-flowered sickle medick (*M. falcata*). The hybrid has strange greenish-black flowers, is exceedingly variable (doubtless owing to Mendelian recombination), but as a group is more vigorous and fertile than either of its parents. In one region of France where lucerne has not been artificially kept up, only the hybrid has survived. Here we have a 'hybrid swarm' so distinct as to merit the separate specific name of *M. sylvestris*.

Plants differ from animals in yet another way, namely their much greater tendency to what is known as polyploidy—the reduplication of whole sets of chromosomes. The chromosomes are the carriers of the genes, which are strung out along their length. The entire hereditary constitution is cut up and divided among a number of chromosomes, the number being normally constant for

[1] A third group in south-eastern Asia also remained black.

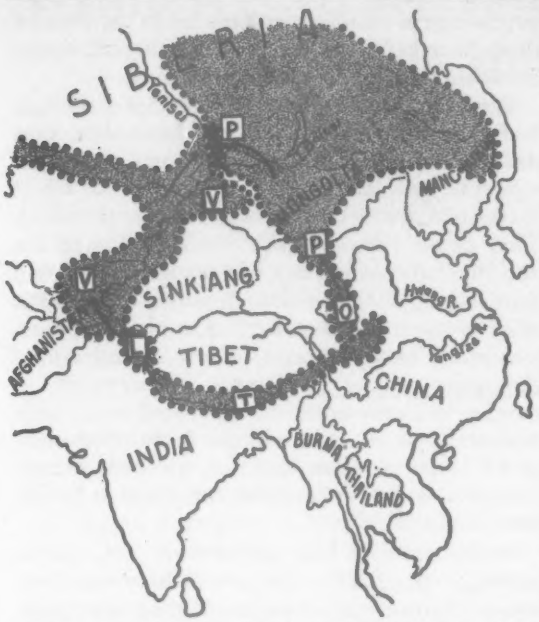


FIGURE 9 – *Subspecies diverging until interbreeding is no longer possible. In central Asia, the warbler* Phylloscopus trochiloides *forms a ring of five closely related subspecies, each intergrading with the next. However, where the two terminal subspecies*—Vizidanus (V) *and* Plumbeitarsus (P)*—have later come into contact, they overlap without interbreeding (cross-hatched area).*

(*From E. Mayr,* Systematics and the Origin of Species. *By courtesy of Columbia University Press.*)

any species. Typically there are two complete sets or packs of chromosomes in each cell of the body; before reproduction, these are sorted out so that each gamete (sexual cell) whether sperm (or pollen-grain) or egg, has one pack only.

The basic number of chromosomes in a single pack is conveniently denoted by *n*. The sexual cells will then contain *n*, the body cells 2*n*. Now sometimes during cell-division the chromosomes may be doubled, but the cell-body fail to divide.[1] All the descendants of this cell will then have double the normal number of chromosomes, or 4*n*; and the shoots and flowers so produced will be *tetraploid*, or four-fold in respect of their chromosomes. Doubling seems to be promoted by extreme conditions, notably cold. Such flowers, crossed with normals, will give 3*n* (triploid) offspring, and these will be sterile, since the chromosomes cannot be distributed to give complete sets in the sexual cells—there will be two of one kind of chromosome, one of another, and the result is a hopeless imbalance. Even if crossed with similar tetraploids, they will have somewhat reduced fertility, since there will be a fair proportion of sexual cells in which division will have distributed three of one kind of chromosome to some cells, and only one to others.

But many plants are capable of non-sexual reproduction—by suckers, bulbils, parthenogenesis, and so forth—and by these means the tetraploids may maintain themselves at first. They are likely to do so, for in difficult conditions they are often hardier than the normal 2*n* (diploid) type.[2] And, once they are established, selection may adjust various mechanisms of cell-division to increase their fertility. Triploids, however, will have to rely entirely on non-sexual methods.

Fresh doubling may later occur, giving 8*n*, 16*n*, 6*n*, 12*n* forms, and so on. Whatever the details of origin, it is a fact that many plants exist in two or more forms which differ primarily in their 'ploidy.' The mountain anemone (*A. montana*), for example, has 2*n*, 4*n*, and 6*n* strains, practically indistinguishable to look at, but incapable of giving fertile or fully fertile offspring when crossed. There is thus *genetic isolation* within the species. But this may become translated into geographical terms. Thus in the cruciferous plant *Biscutella laevigata*, the original 2*n* type has been able to survive only in a few isolated areas. The 4*n* type, which may well have arisen in the first place owing to the cold, was also more cold-resistant and more generally vigorous; it now occupies a large continuous area across Europe, reaching a good deal further north than the 2*n* type. Sometimes the evidence suggests that the original 2*n* forms have been wholly unable to compete with the 4*n*'s, and have simply died out.

Here is quite a new method of diversification. In animals, some degree of genetic isolation may come about through internal rearrangements of bits of the chromosomes (too complex to describe here), and if aided by geographical isolation may lead on to the separation of mutually infertile groups—true species—which will tend to resemble each other very closely.

CONVERGENT SPECIES-FORMATION: NETWORK CLASSIFICATION

The most surprising fact about plant evolution, however, is that definite new species can be formed abruptly, by the crossing of two other species followed by chromosome-doubling. We

[1] Or a gamete may be formed with the unreduced (2*n*) number of chromosomes.

[2] Chromosome-doubling also not infrequently produces an increase of size of the whole plant or of its organs.

may call this convergent species-formation, as opposed to the usual splitting or divergence of one species into two or more.

The classical case is that of *Primula kewensis*, so called because it arose at Kew from a spontaneous cross between two well-known species, *P. verticillata* and *P. floribunda*. It was at first entirely sterile, but after some years of cultivation by cuttings, a single fertile shoot appeared. When examined, this was found to possess 36 chromosomes instead of the 18 of the rest of the plant and of both its ancestors. Before doubling, the hybrid had one pack of chromosomes from each parent. And these were so different that they would not work together properly. But after doubling it possessed two complete double packs; and now sexual reproduction with reasonably normal chromosome-pairing and normal development could take place (see also figure 5). A tetraploid produced thus is called an allotetraploid, as opposed to the autotetraploids or self-doublers previously considered.

Primula kewensis probably owes its survival to human aid. But *Spartina townsendii* shows what may occur (figure 7). *Spartina stricta* is a European rice-grass of salt-marshes. *S. alterniflora* is an American species whose seeds were accidentally brought over in ships' cargoes. The two seem to have crossed ($n = 28$) × ($n = 35$); but the resultant hybrid ($2n = 63$) must have been infertile until it doubled its chromosome-number to 126. This new tetraploid species is hardier than either parent, and is able to colonize tidal mud-flats where neither would previously grow.

The pink garden horse-chestnut arose in a similar way from a cross between the white-flowered European horse-chestnut and the American red buck-eye.

Polyploidy, auto- and allo-, singly and in combination, has undoubtedly played a large part in the evolution both of wild and cultivated plants.

Finally we must mention some groups, such as the blackberries and the willows, where sexual and asexual reproduction, hybridization, and both kinds of polyploidy are combined in such a way that an interlocking network of forms is produced, with lines of descent both converging and diverging. The results defy all attempt at ordinary pigeon-holing, so that the species-concept largely breaks down in such networks.

The only animal in which anything approaching this 'reticulate' evolution occurs is man. If man had been like other mammals, we can be sure that his major 'races' would have diverged along fully separate paths. But his restlessness and his psychological peculiarities have led to the original divergence being replaced by a steadily increasing amount of migration and intercrossing.

Between one and two million species of animals and plants are known. As we have seen, they differ in their mode of origin, their size, their structure and variability, their capacity to adjust themselves to new conditions or to become extinct. They clothe the world in diversity. New species and new adaptations are still being evolved, and contributing to this minor diversity of life. But what of the major diversity? Are new long-term trends still being initiated, which are capable of producing wholly new types of organism—as novel as the horse or the cat compared to the early mammals; as the warm-blooded mammal compared to its reptilian ancestor; as land animals compared to fish; as flowering compared to flowerless plants?

No one can give a certain answer. Yet it seems probable that life's major trends have run their course. It is a rule of evolution that new major types become dominant by branching out into lines of increasing specialization and that each specialization eventually comes to a dead end. Selection can push it no further along that line—it can merely ring minor changes upon the type by throwing off new species or genera. And when a new dominant type arises, it does so from an unspecialized member of the previously dominant group.

There is one exception to this—the human species. Man is now the dominant type of organism. He has remained unspecialized in structure. He has not radiated out into wholly separate lines. His new capacities for conscious thought and purpose, on which his biological dominance depends, give him the possibility of establishing a common pool of consciousness. His specializations are learnt, not inherited biologically. If he set his mind to it, he could control not merely his natural and his social environment but his future biological evolution.

The study of species is providing part of the essential knowledge which he must amass. During the last few decades, the advances in genetics, cytology, and other branches of biology have made a new, synthetic view possible. The patient and too often unrecognized labours of the museum classifiers are bearing fruit, and are being extended into the field and the experimental laboratory. Within a short space of time, the materials will be ready for a new Darwin to write another masterpiece on the subject—but the title will have to be not the *Origin*, but the *Origins of Species*.

William Curtis, founder of *The Botanical Magazine*

J. W. HUNKIN

Scientific journals, as one of the main channels for the exchange of information and opinion, have played an important part in the development of science. It is appropriate that in this year, which sees the second centenary of his birth, we should remember the work of William Curtis, founder of *The Botanical Magazine*. This was one of the earliest botanical journals; its publication has not been interrupted since its first appearance in 1787, and in its own field it has established a reputation as one of the world's foremost periodicals.

William Curtis, founder of *The Botanical Magazine*, was born at Alton, in the English county of Hampshire, on 11th January, 1746. His father was a tanner and a member of the Society of Friends. At the age of fourteen, William was apprenticed to his grandfather, John Curtis, the surgeon-apothecary of Alton, whose premises were next door to the Crown Inn. An ostler employed at this inn had a remarkable knowledge of the wild flowers and the insects of the neighbourhood, and encouraged the boy in his taste for natural history. When he was twenty, William was sent to London, to assist an apothecary and to study at St. Thomas's Hospital; but natural history remained his chief interest, and on one occasion he was taken severely to task for paying three guineas for an engraving of the common nettle.

When his employer died he succeeded to his business, and a trade card declares that 'William Curtis, Apothecary, 51, Gracechurch Street, sells all sorts of drugs and chemical medicines.' Some years ago the Corporation of the City of London placed a plaque of blue encaustic on the wall of the tall building which now occupies the site:

'In a house on this site lived
WILLIAM CURTIS, Botanist,
B. 1746 – D. 1799.'

It is pleasing to observe that the plaque has survived the war undamaged.

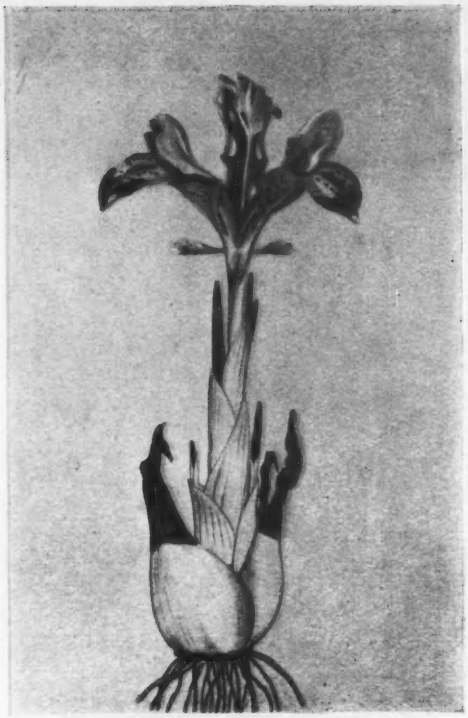
In 1770 Curtis took a partner, and not long afterwards sold him the practice. In the next year, with the support of two London business men, Benjamin and Thomas White, brothers of the Rev. Gilbert White of Selborne, Curtis started a garden of about an acre in Grange Road, Bermondsey, for the cultivation and study of British plants.

This year, 1771, saw the first of Curtis's publications, a pamphlet of 44 pages with one plate. It was entitled ***Instructions for collecting and preserving insects; particularly Moths and Butterflies***. This little work received the commendation of Mr Banks (afterwards Sir Joseph), and his friend and secretary, Dr D. C. Solander.

In 1772, Curtis was appointed Demonstrator of Botany to the Society of Apothecaries at Chelsea. It was his duty to show the young apprentices the medicinal plants in the Apothecaries' Garden, and to take them on botanical excursions in the neighbourhood. He threw himself into this work with great zest.

In May, 1775, there appeared the first number of the *Flora Londinensis*, 'A new and original Botanic Work, intended to comprehend all the Plants which grow wild in Great Britain, beginning first with those which are found *in the environs of London*.' Partly from lack of funds, and partly through pressure of other work, the numbers (which were priced at five shillings coloured and half a crown plain) appeared with an irregularity which exasperated the subscribers, and the sale seldom, if ever, exceeded three hundred copies. Of the seventy-two numbers, only two contained descriptions of plants from localities more than ten miles from London. The entire publication, which was ultimately bound up in two monumental volumes, was abandoned in 1798.

In 1777, Curtis resigned his appointment as Demonstrator, and in the same year published a students' edition of Linnaeus's *System of Botany*. Two years later, on 1st January, 1779, he opened a 'London Botanic Garden' at Lambeth Marsh. Subscribers of one guinea a year were entitled to walk in the Garden every day except Sunday, use the library, and introduce one person. Those subscribing two guineas could introduce more than one, either in person or by ticket, and receive



Iris persica (*t.*1).

Erica ciliaris (*t.*484).

Camellia japonica (*t.*42).

Jasminum officinale (*t.*31).

(*Illustrations taken from early volumes of* The Botanical Magazine.)

roots and seeds of such plants as could be spared without diminishing the necessary stock. A catalogue of the plants, about six thousand in number, was issued in 1783. It was divided into five sections: medicinal plants, culinary plants, common poisonous plants, agricultural plants, and British plants. It contained a list of persons to whom Curtis was indebted for plants to start the garden. This began with Mr Aiton of Kew, and included Sir Joseph Banks, the Rev. J. Lightfoot, the Rev. Dr Goodenough, Mr James Crowe of Norwich, Mr Thomas Woodward of Bungay, and several of the leading nurserymen such as Lee (who introduced the cultivation of the fuchsia into England) and Loddiges.

The need for such a garden will be appreciated when it is realized that at this time even the Physic Garden at Oxford was 'neglected and deserted' —I quote from a letter dated 21st May, 1778, written by a Mr J. Stokes of Worcester, who had just been to see it.

In 1782, great alarm was created by the appearance of vast numbers of the brown-tailed moth. 'In many of the Parishes of London, subscriptions were opened, and the poor people employed to cut off and collect the webs, at one shilling per bushel, which were burned under the inspection of the Churchwardens, overseers, or beadle of the parish. At the first onset of this business, four score bushels, it is stated upon creditable authority, were collected in one day, in the parish of Clapham. They were supposed to be the forerunner of the plague: even prayers were offered up in some churches, to deliver us from the apprehended calamity.'[1] Accordingly, Curtis published a monograph on the insect, price one shilling and sixpence, in which he clearly showed how ill-founded the alarm was.

It was five years later, in 1787, that Curtis began to issue what proved to be by far his most important publication, *The Botanical Magazine*, now often referred to as *Curtis's Botanical Magazine*. The inaugural number appeared on 1st February, with the title page shown overleaf.

Portrait of William Curtis by Wright.
(Reproduced by permission of the Royal Horticultural Society.)

In his preface to *The Botanical Magazine* Curtis lays down a principle which has been followed in the *Magazine* ever since:

'At the commencement of this publication, he had no design of entering on the province of the Florist, by giving figures of double or improved flowers, which sometimes owe their origin to culture, more frequently to the sportings of nature; but the earnest entreaties of many subscribers have induced him so far to deviate from his original intention as to promise them one at least of the Flowers most esteemed by Florists.'

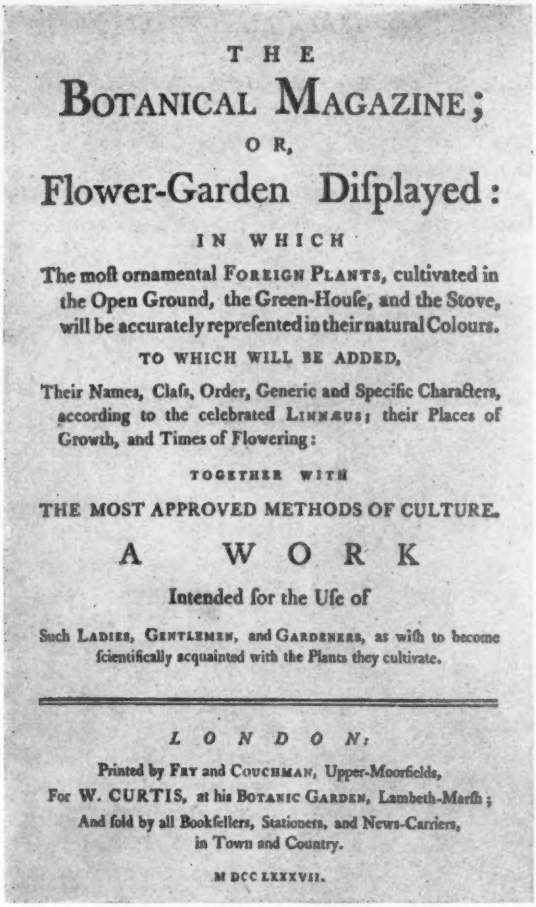
Curtis used to say that the *Flora* brought him praise, but *The Botanical Magazine* brought him pudding—and eventually praise more abundant also. For the *Magazine* not only flourished during his lifetime but has continued to do so down to the present day, the latest volume to be published being Vol. CLXIV, 1944, and the last plate being numbered t.9666. It was originally issued in monthly numbers (octavo), each containing three plates and descriptions of plants and costing one shilling. It was the first illustrated botanical periodical, and was an immediate success. It had a sale of about 2,000 monthly copies, which soon increased to 3,000.

A brief letter (31st December, 1789) from Dr Goodenough, one of the founders of the Linnaean Society, and afterwards Bishop of Carlisle, illustrates the appreciation with which the *Magazine* was at once received:

'Dear C.U.R.,

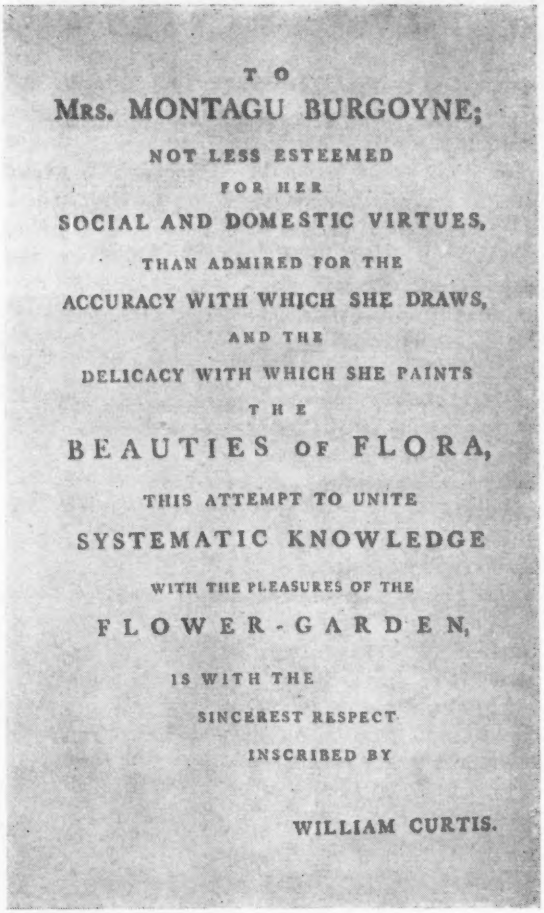
'The Duchess of Portland begs that you would *immediately* upon receipt of this, send her the thirteenth number of the *Botanical Magazine* and ever afterwards the other numbers as they are published, on the very day on which they are published. You are to leave them at Burlington

[1] Dr R. J. Thornton, *Sketch of the Life and Writings of W. Curtis*, pp. 4, 5.



THE
BOTANICAL MAGAZINE;
OR,
Flower-Garden Displayed:
IN WHICH
The moſt ornamental FOREIGN PLANTS, cultivated in the Open Ground, the Green-Houſe, and the Stove, will be accurately repreſented in their natural Colours.
TO WHICH WILL BE ADDED,
Their Names, Claſs, Order, Generic and Specific Characters, according to the celebrated LINNÆUS; their Places of Growth, and Times of Flowering:
TOGETHER WITH
THE MOST APPROVED METHODS OF CULTURE.
A WORK
Intended for the Uſe of
Such LADIES, GENTLEMEN, and GARDENERS, as wiſh to become ſcientifically acquainted with the Plants they cultivate.

LONDON:
Printed by FRY and COUCHMAN, Upper-Moorfields,
For W. CURTIS, at his BOTANIC GARDEN, Lambeth-Marſh;
And ſold by all Bookſellers, Stationers, and News-Carriers, in Town and Country.
M DCC LXXXVII.



TO
MRS. MONTAGU BURGOYNE;
NOT LESS ESTEEMED
FOR HER
SOCIAL AND DOMESTIC VIRTUES,
THAN ADMIRED FOR THE
ACCURACY WITH WHICH SHE DRAWS,
AND THE
DELICACY WITH WHICH SHE PAINTS
THE
BEAUTIES OF FLORA,
THIS ATTEMPT TO UNITE
SYSTEMATIC KNOWLEDGE
WITH THE PLEASURES OF THE
FLOWER-GARDEN,
IS WITH THE
SINCEREST RESPECT
INSCRIBED BY
WILLIAM CURTIS.

Title-page and dedication from The Botanical Magazine, *Vol.* I, 1787.

House, Piccadilly. Her Grace is beginning to be very botanical.'

Fourteen volumes were issued during the first period of the history of the *Magazine*, which extends to the founder's death in 1799. They contain 504 plates drawn by Sydenham Edwards. Edwards continued to illustrate the *Magazine* after Curtis's death till he withdrew in 1815. By that time he had produced nearly 1,770 drawings. Curtis's colourist was William Graves, and his rendering of the delicate graduation of colours in flowers is often charming. Many of his colours have stood the test of time very well, but some of the whites and heavy reds have faded. The plants illustrated and described are mostly hardy European and North American, together with *Erica*, *Pelargonium*, *Mesembryanthemum* and *Gladiolus* from South Africa. It should be remembered that in 1772 William Masson had been sent out from Kew to the Cape and had thence introduced a large number of plants.

The first plate gives an attractive figure of *Iris persica*. The description is short, and includes the following sentences: 'Its beauty, early appearance, and fragrant blossoms, make it highly esteemed by all lovers of flowers; like the Hyacinth or Narcissus it will grow within doors in a water-glass, but stronger in a small pot of sand, or sandy loam; a few flowers scent a whole apartment; it will also blossom in the open air, but requires warmth and shelter.' Curtis takes pains with his phrases, and his prim, smoothly-rounded style is distinctly pleasing. 'This charming shrub,' he writes of *Coronilla glauca* (t.13), 'which is almost perpetually in blossom, and admirably adapted for nosegays, is a native of the South of France, and a constant

ornament of our green-houses.' 'There is an elegance in the Jasmine,' he says of *Jasminum officinale* (t.31), 'which, added to its fragrance, renders it an object of universal admiration.' 'The blossoms' (of *Camellia japonica* (t.42)), 'are of a firm texture, but apt to fall off long before they have lost their brilliancy; it therefore is a practice with some to stick such deciduous blossoms on some fresh bud, where they continue to look well for a considerable time.' *Colutea arborescens* (t.81) 'produces a profusion of bloom from June to August, when its inflated pods please from the singularity of their appearance.'

Volume V, 1791, includes the figure of *Sophora tetraptera*, discovered by Sir Joseph Banks in New Zealand and planted by Mr Forsyth about 1774 in the Apothecaries' Garden at Chelsea, 'now extending' (28th April, 1791) 'to a great breadth on a wall with a West aspect, thickly covered with large pendulous branches of yellow flowers (of peculiar richness).'

Among other notable items in this first series may be mentioned *Pelargonium tricolor* (t.240), here first described (Vol. VIII, 1794); *Metrosideros citrina* (t.260, *Callistemon lanceolatus*), the forerunner of many brilliant Australian shrubs, believed by Curtis to be the first that had flowered in England; *Rosa semperflorens* (t.284), which he regarded as one of the most desirable ornamental plants ever introduced into England, actually a variety of *Rindica*—both these in Vol. VIII, 1794; and *Cineraria cruenta* (t.406) from the Canary Isles, the parent of the great variety of florists' cinerarias (Vol. XII, 1798). A beautiful plate is that of *Erica ciliaris* (t.484), a native of Spain and Portugal (Vol. XIV, 1800).

In 1788, the Linnean Society was founded, with Dr Goodenough as Treasurer. Curtis's signature appears third on the Roll Book. During the following year, Curtis moved his plants to a new Botanic Garden at Brompton. He had been greatly troubled, he says, at Lambeth Marsh by the smoke of London, the obscurity of the situation, and the badness of the roads leading to it, as well as 'with the effluvia of surrounding ditches, at times highly offensive.' The new garden occupied about three-and-a-half acres and included greenhouses and a library. A subscription catalogue of the Brompton Botanic Garden was issued in 1792–93. The garden was carefully planned and divided into various quarters: medicinal, agricultural, foreign grasses, British grasses, British trees and shrubs, and so on. Surrounding these were 'all the foreign trees and shrubs, which are able to be naturalized in our climate, and which beautifully decorate, shade and screen the whole.'

A pamphlet issued by Curtis in 1792 contained proposals for a course of herbarizing excursions during the summer months in Battersea meadows. The fee for the course was two guineas. Dr Thornton, who went botanizing with him, says 'His eye was truly microscopic . . . when herbarizing with a large party his keen sight always collected twenty times as many different plants as were obtained by the whole company.'

In 1799, Curtis published a pamphlet on the cultivation of seakale for the use of the table. With each pamphlet he sold a box of seed in his desire to bring the plant into common cultivation. His attention had been called to it by his friend, Dr Lettsom, who had found it eaten by fishermen near Southampton.

Dr Thornton and Dr Goodenough both left descriptions of their friend. He was short and thick-set, ruddy in face, and abounding in good humour. 'I have no pretensions,' he said of himself 'to be considered as a man of letters, or of great mental powers, I know myself and my imperfections. A consciousness of my inabilities makes me diffident, and produces in me a shyness, which some have been ready to construe into pride.'

On 7th July, 1799, Curtis died suddenly of heart failure, and was buried in Battersea (old) Churchyard, opposite the West entrance. The following inscription was placed on the tombstone:

'Here are deposited the remains of Mr William Curtis, Author of the *Flora Londinensis*, and the *Botanical Magazine*, and other works highly serviceable to his country, and honourable to himself.

He died July 7th, 1799, aged 53 years.

"While living herbs shall spring, profusely wild,
Or garden cherish all that's sweet and gay;
So long thy works shall praise, dear Nature's child,
So long thy memory suffer no decay."'

The inscription has become entirely defaced, but it is hoped to renovate it in time for a memorial service in Battersea Parish Church on the Sunday nearest to 11th January, 1946 (i.e. Sunday, 13th January).

The latest biography of William Curtis was published in 1941 by Mr W. Hugh Curtis, Curator of the Curtis Museum, Alton. Mr Hugh Curtis has been able to make good use of a number of letters hitherto unpublished, and his comprehensive work will long remain the standard biography. I have freely drawn upon it in this brief account.

Electric lighting by luminescence

C. C. PATERSON

Electric lamps of the familiar filament type possess various shortcomings, but it seems unlikely that they are susceptible of much further improvement. Interest therefore centres on the modern method of electric lighting by luminescence, which promises to effect an even greater revolution in illumination than did the introduction of the metal filament lamp some thirty years ago. Dr Paterson here describes and explains some of the main phenomena involved.

INTRODUCTION

The chief technical advance in electric lighting during the past twenty-five years has a dual origin. The first is the property possessed by electric discharges through certain vapours to radiate relatively large proportions of their energy in the visible or ultra-violet regions of the spectrum. The second is the property possessed by certain luminescent materials to fluoresce very strongly when in contact with the discharge.

The luminous efficiencies of temperature radiators have probably reached their practical limit in the gas-filled tungsten filament lamp, and only minor improvements in such light sources can be expected. It will be informative to examine the factors which encouraged the belief that at least equally efficient lamps of other types could be produced.

These factors can be made clear by a study of the diagram (figure 1) showing the distribution of spectral energy in the radiation from a hot tungsten filament, and in that from an electric discharge through low pressure mercury vapour. It will be seen that the radiation from the tungsten filament is continuous and that the peak of the emission occurs in the infra-red or heat region; furthermore, very little ultra-violet radiation is emitted. The proportion of energy emitted in the visible region depends on the temperature of the filament, but at temperatures giving a reasonable life only about 10 per cent. of the input energy appears as light, corresponding to a luminous efficiency of approximately 15 to 20 lumens per watt.

The spectral energy curve of the mercury vapour discharge shows that the radiation is no longer continuous but occurs as narrow spectral lines; a high proportion (some 50 per cent.) of the input energy is emitted in the invisible ultra-violet at a wavelength of 2537 A. In spite of the virtual absence of invisible infra-red radiation from the spectrum of the mercury discharge, its efficiency in lumens per watt is even poorer than that of a filament lamp. The important factor is, however, that the ultra-violet energy of the mercury discharge can be converted into visible radiation by means of luminescent materials, resulting in sources giving white light at efficiencies as high as 60 lumens per watt. It is with such sources that the present article is primarily concerned.

LUMINESCENT MATERIALS AND THE MECHANISM OF LUMINESCENCE

Luminescent materials include fluorescent and phosphorescent substances, the latter being characterized by a continuance of the glow for a time after the stimulation has stopped. These luminescent substances may be regarded as frequency changers of electro-magnetic waves. The change is always from short to longer wave-lengths, and there are, unfortunately, no equivalent conditions or materials which enable the longer wave infra-red heat radiation to be converted into the shorter wave visible radiation. It is for this reason that luminescent materials cannot be used to improve the efficiency of tungsten filament lamps.

Many substances are luminescent to some degree. Mineral oils,. some organic substances such as anthracene and quinine, and certain dyestuffs are strongly fluorescent; certain minerals, of which the best known are perhaps willemite, or zinc orthosilicate, and fluorite, or calcium fluoride, also show strong luminescence. Figures 2 to 4 show reproductions from actual colour photographs of some of these substances stimulated by radiation of wavelength 3650 A.

Apart from their use in conjunction with black glass lamps to obtain certain spectacular effects, these materials have no serious application in artificial lighting. Naturally occurring inorganic luminescent materials are too rare, and are in any case too inefficient, to have any practical

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XI

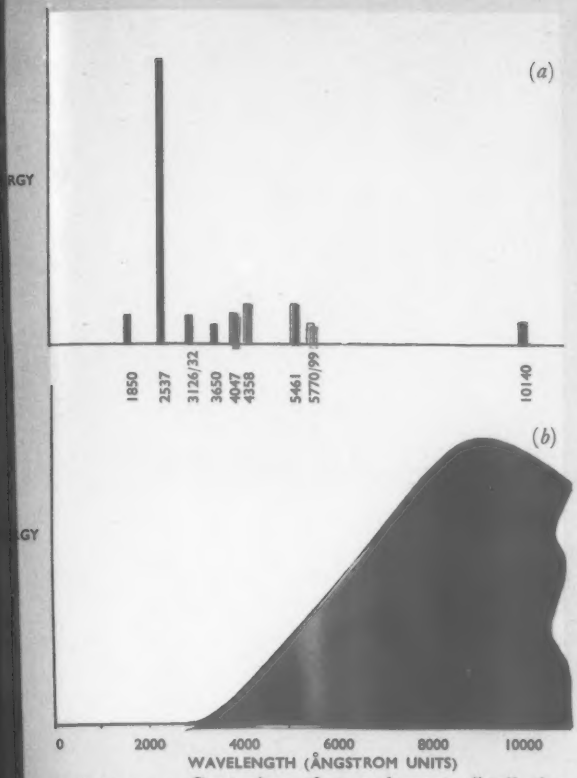


FIGURE 1 – *Comparison of spectral energy distribution of the radiation emitted by an electric discharge and an incandescent tungsten filament. (a) Low pressure mercury vapour discharge. (b) Incandescent tungsten filament.*

FIGURE 2 – *Luminescent streamers produced by dusting fluorescent dyes (fluorescein and rhodamine) into water irradiated by 3650 A radiation.*

value. The luminescent salts used in discharge lamps are therefore synthesized in the laboratory, either by conventional precipitation methods or by direct union of the dry acidic and basic constituents at a high temperature. In each method exceedingly high purity is necessary, and the material must be fired in special furnaces at temperatures as high as 1,200° C to develop the essential crystalline structure. Before firing, the material is treated with a small quantity of a metallic activator—very often manganese. A range of fluorescent colours is obtained by using different parent compounds or matrices, and sometimes different activators. Table I gives a list of some of the more important luminescent compounds. Figure 5 shows a reproduction in colour of some of these materials stimulated by ultraviolet radiation.

TABLE I

LIST OF MAIN LUMINESCENT POWDERS

Matrix	*Activator*	*Fluorescent Colour*	*Exciting Wavelength*
ZnS	Ag	Blue	3650 A
ZnS	Cu	Green	3650 A
(Zn,Cd)S ..	Cu	Yellow-red	3650 A
Zn_2SiO_4 ..	Mn	Green	2537 A
$(Zn,Be)_2SiO_4$	Mn	Yellow-red	2537 A
CdB_2O_4 ..	Mn	Red	2537 A
$MgWO_4$ ..	Self-activated	Blue	2537 A

The mechanism of luminescence is exceedingly complex, and has as yet been explained only in qualitative terms. Very briefly, modern theory assumes that the activating atoms form so-called active centres in the crystalline matrix, in which the atoms of the activator are more or less isolated

FIGURE 3 – *Artificial silk dyed with various fluorescent dyes and excited by 3650 A radiation. In the powder form these dyes are not luminescent but become so when dispersed in a suitable solvent or fabric.*

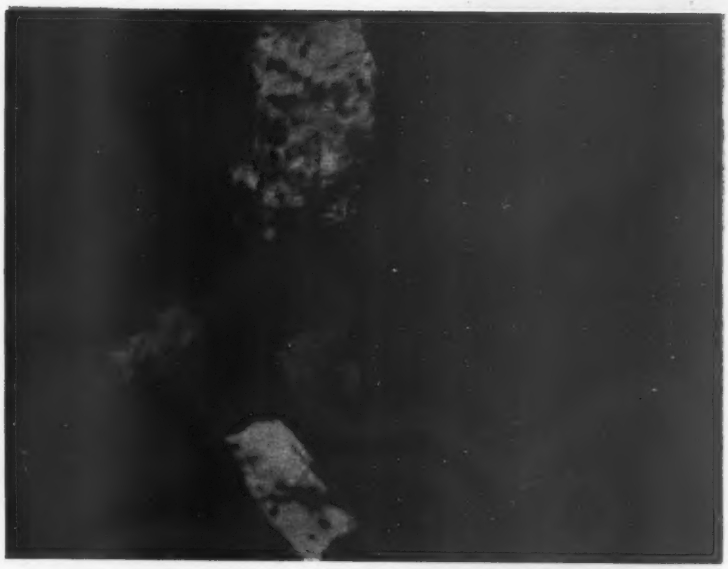


FIGURE 4 – *Luminescent minerals under 3650 A radiation. Luminescence in natural substances is not, as a rule, very well developed. The minerals shown here are exceptional in that they exhibit marked luminescent effects.*

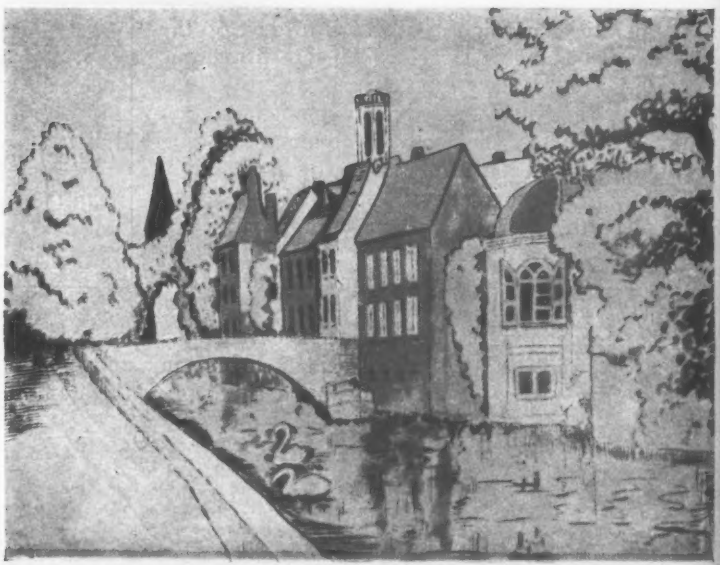


FIGURE 7 – *Picture painted with luminescent sulphides viewed in normal light. The drab appearance is due to the lack of natural colour in the luminescent pigments.*

FIGURE 5 – *Synthetic luminescent powders excited by long-wave ultra-violet radiation. The powders are mainly zinc and zinc-cadmium sulphides activated by silver and copper.*

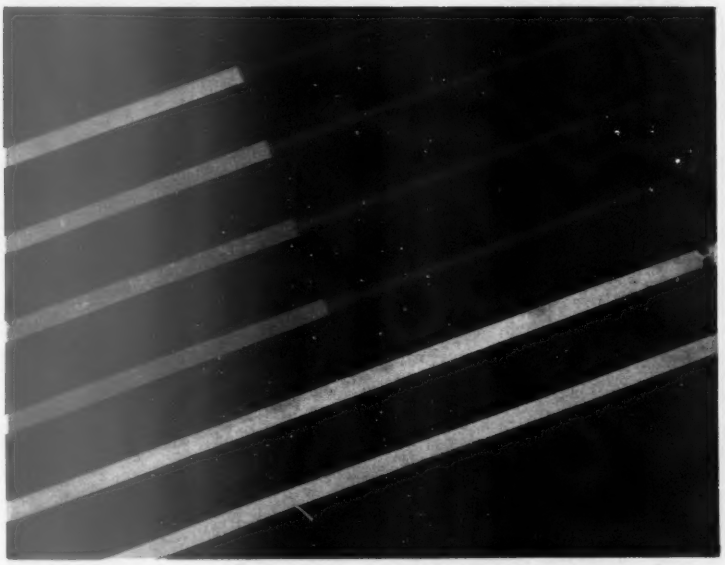


FIGURE 6 – *Fluorescent lamps coated with various fluorescent powders. Some of the tubes have been left uncoated over half their length to show the colour of the unmodified discharge. The bottom two lamps have been coated with blends of powders to give daylight and warm white effects.*

FIGURE 8 – *The same picture irradiated by long-wave ultra-violet radiation.*

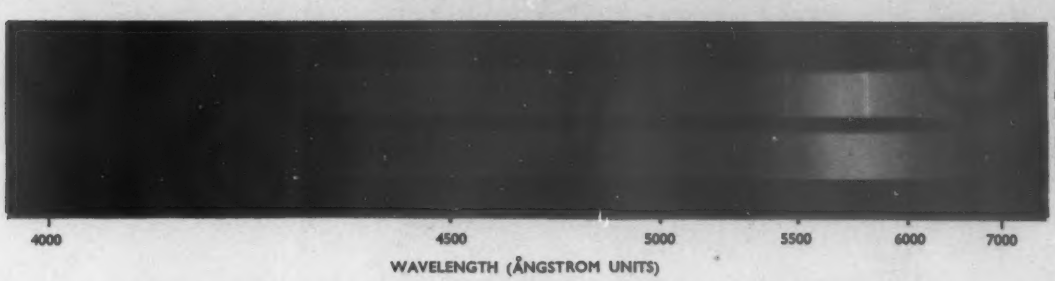


FIGURE 9 – *Spectrum of daylight fluorescent lamp compared with that of natural daylight. Mercury lines superposed on the continuous background will be noted in the former spectrum. The Fraunhofer absorption lines in the daylight spectrum can also be seen.*

from their fellows by the molecules of the crystalline lattice. This enables them to absorb and emit energy by transition of electrons between energy levels which are, however, associated also with the molecular arrangements in the crystal. Thus, instead of fine spectral lines resulting from transitions between discrete energy levels, as in electric discharges, the energy levels give rise to radiation covering a range of wavelengths.

LUMINESCENT EFFECTS WITH BLACK GLASS LAMPS

Apart from their use in discharge lamps, with which the present article is primarily concerned, certain luminescent powders have come into use for providing spectacular lighting and display effects in conjunction with black glass lamps. Figure 8 shows a picture painted with sulphide phosphors viewed under black lamp radiation, while figure 7 shows the same picture under ordinary white light.

It is interesting to note that with normal paints and pigments subtractive mixtures of light are obtained. Thus a yellow pigment is yellow because it absorbs blue and, as everyone knows, a mixture of blue and yellow paints gives green. In mixing luminescent pigments however, the artist has to deal with an additive mixture of lights, and blue and yellow luminescent materials do not give green when mixed, but white. It is, of course, necessary for the artist to mix his luminescent pigments and to use them under ultra-violet radiation with visible light excluded as far as possible. With a little practice the new technique is easily acquired.

It has often been proposed to use, as sources of illumination, large areas such as walls and ceilings coated with luminescent materials and irradiated by black glass lamps. This form of illumination has interesting possibilities for decorative purposes, but is hardly likely to come into use for general lighting because of its high cost and low luminous efficiency, the latter amounting to only one or two lumens per watt.

THE LUMINESCENT COATING

In practical fluorescent lamps the luminescent material is applied, usually suspended in a suitable organic binder, as a thin uniform coating to the inside surface of the tubular envelope. The binder is removed by heat during the processing of the lamp; this leaves the powder layer exposed to the direct action of the ultra-violet radiation emitted by the discharge. Owing to the need for keeping the pressure of the mercury vapour low, in order to secure the maximum output of ultra-violet radiation, fluorescent tubular lamps operate not much above normal ambient temperatures, and for this reason are generally large in relation to their consumption of power.

Figure 6 shows a number of fluorescent lamps 5 feet long and 1½ inches in diameter, each rated at 80 watts. Some of these lamps have been coated with various luminescent powders over half their lengths only, the other half being left uncoated to show the mercury discharge. It will be seen that the fluorescent coating glows so brightly that the light from the mercury vapour itself is almost completely masked by the resulting luminescent glow.

To obtain white colours of spectral energy distribution approximating to that of the sun, it is usual to employ coatings comprising mixtures of individual powders. Two such white lamps are shown at the bottom of figure 6. It is interesting to record that recent developments in this country have resulted in single luminescent compounds which give, by themselves, satisfactory white

DAYLIG
LUORE
AMP.
NATURA
DAYLIG

colours. The similarity between the spectrum of a daylight fluorescent lamp and that of natural daylight is shown in figure 9. The line radiation in the former spectrum corresponds to only about 10 per cent. of the total visible radiation, and does not appreciably distort the colour rendering of the light.

THE QUANTUM EFFICIENCY OF LUMINESCENT MATERIALS

In considering the possibility of future developments it is important to estimate what percentage of the theoretical maximum of efficiency is achieved by modern luminescent powders. A luminescent substance is said to be 100 per cent. efficient if it emits one quantum of radiation for each quantum absorbed; but it must be remembered that, since the energy in a quantum of radiation is inversely proportional to the wavelength, there is an inevitable loss of energy in transforming ultra-violet radiation into white light. This amounts to approximately 50 per cent. for ultra-violet radiation of wavelength 2537 A.

The quantum efficiency of a powder depends on the method of preparation, and on the precautions taken with regard to purity and related factors. It is obvious, for instance, that a luminescent powder having considerable body colour is likely to have a lower quantum efficiency than a similar powder free from body colour. Quantum efficiencies can be determined from the measured luminous efficiency of fluorescent lamps of known spectral energy distribution dissipating a known amount of ultra-violet energy: values as high as 85 to 90 per cent. are usual. It will be seen, therefore, that further considerable improvements in the efficiency of fluorescent lamps by improvements in the quantum efficiency of the powders can hardly be expected.

LUMEN MAINTENANCE OF FLUORESCENT LAMPS

The above remarks refer to powders in their initial state before the lamp has been in operation for any appreciable time, and it is not to be inferred that no further improvement in the powder is possible. One of the less desirable characteristics of mercury-filled fluorescent lamps is the fall in light output as the lamp is run; this is due to the formation of deposits of mercury and mercury compounds on the fluorescent coating under the action of the discharge. The slow disintegration by the discharge of the material of the filament, part of which deposits on the coating, is also a contributory factor. The film so formed absorbs some of the ultra-violet radiation, and thus, of course, reduces the efficiency of the lamp. The fall is most rapid during the early part of the life of the lamp and thereafter proceeds more slowly. It depends to some extent on the current density: with lamps of fairly high current density, such as the British 80 watt lamp, it may amount to 20 per cent. during the first few hundred hours and a further 20 to 30 per cent. during the subsequent 3,000 hours.

A number of factors influence the rate at which the absorbing film on the coating is formed; among them may be mentioned the nature of the luminescent material itself. This aspect of powders is receiving close study, and it is from this point of view that the greatest improvements in luminescent powders are likely to arise.

PRACTICAL FLUORESCENT LAMPS

Table II gives the wattages and dimensions of fluorescent lamps likely to be marketed in Britain within the next year or so. These lamps will be available in a daylight colour and also in a warm white colour for more restful lighting. Both colours are shown in figure 6.

TABLE II

DIMENSIONS AND WATTAGES OF BRITISH FLUORESCENT LAMPS

Nominal Lamp Dimensions		*Lamp Wattage*
Length (feet)	*Diameter (inches)*	
5	1½	80
4	1½	40
3	1	30
2	1½	20
2	1	20
1½	1	15

The average efficiencies and lives of fluorescent lamps are from two to three times those of ordinary tungsten lamps. It may be said, too, that the special characteristics of colour and diffusion possessed by fluorescent lamps, although difficult to measure, rank as high as luminous efficiency in importance to the illuminating engineer, and to the numerous users who show aesthetic discrimination. Fluorescent lamps are already well established for industrial and commercial lighting.

Some aspects of dairy bacteriology

A. T. R. MATTICK

Dairy bacteriology is a comparatively young branch of applied science, but it is rapidly growing in importance and already has much success to its credit. Its main concern is with milk itself, a foodstuff with a unique role in human nutrition, but one which unfortunately is too often contaminated by harmful bacteria. To ensure the supply of dietetically safe milk is not, however, the dairy bacteriologist's only aim, and the present article describes various other aspects of modern work, much of which has notable scientific interest.

Cow's milk plays a unique role in the diet of most civilized peoples. The cow converts vegetable products in large quantities into first-class protein, fat, and carbohydrate, and blends them in water with the necessary inorganic salts and vitamins in such a way that milk is almost a complete food. Milk is also an admirable medium for the growth and survival of many kinds of bacteria, and the bacteriology of milk and its products is a rich field for investigation. It is not possible here to deal with more than certain aspects of the subject. Microbiologists, as recent publications show, are beginning to appreciate the importance of the study of the effect of physical factors and environment upon the constitution and metabolism of micro-organisms. In a mixed population of bacteria many factors, not least the growth products, among which are antibiotic substances, determine the predominance of types, and it is proposed to give some account of their interactions.

PASTEURIZATION

Although great technical advances, actual and potential, have been made in the preparation of dried and otherwise preserved milk, it is likely that the demand of the public for fresh liquid milk will continue to expand in spite of the strength of the argument that, as milk contains some 87 per cent. of water, it is uneconomical to transport and distribute it in its natural form. For hygienic reasons, the fact that milk is so distributed imposes heavy responsibilities on the producer and seller of milk.

If all the micro-organisms which may be present in milk were non-pathogenic to man and animals, the spoilage which they cause might be accepted as merely inconvenient and wasteful. But this is not so, since cows themselves suffer from bacterial diseases such as tuberculosis, contagious abortion, streptococcal and staphylococcal mastitis, and even *Salmonella*-enteritis, all of which are communicable to man. The only safe, satisfactory, and economical method of killing these organisms is by pasteurization, which makes use of the fact that if maintained at temperatures in the region of 60° C for approximately 10 to 15 minutes, or an equivalent combination of temperature and time, the vital protoplasm of vegetative bacteria is denatured and the organisms are killed. The numbers of animals suffering from the more serious of these diseases in a dangerous form may be relatively small, but when the milk of several herds is mixed the dangers of infecting large numbers of consumers are patent.

It is, of course, possible—though difficult—to produce milk which is free from organisms causing some of these animal diseases, but the chance is always present that the milk may be subsequently infected with a variety of organisms from human sources.

The elimination of pathogenic organisms is accepted as the main reason for pasteurization, but at the same time most of those causing souring and other faults are destroyed as well. The microbial life of the milk has to start afresh after pasteurization, so that it is possible to provide city dwellers with unsoured milk—a virtual impossibility with raw milk when the 'milk-shed' is at a distance from the centre of distribution.

THE AËROBIC SPORE-FORMERS

The process of pasteurization itself provides many interesting problems in bacteriology. Ordinary raw market milk may contain considerable numbers of organisms in great variety, but in practice the greater part of the flora is confined to comparatively few types: 'lactic' and other streptococci, coliform organisms, micrococci, and some spore-forming types. The latter are probably ultimately derived from the soil. Farm and factory utensils and apparatus are normally sterilized by steam, which, properly applied, kills all

VISTA

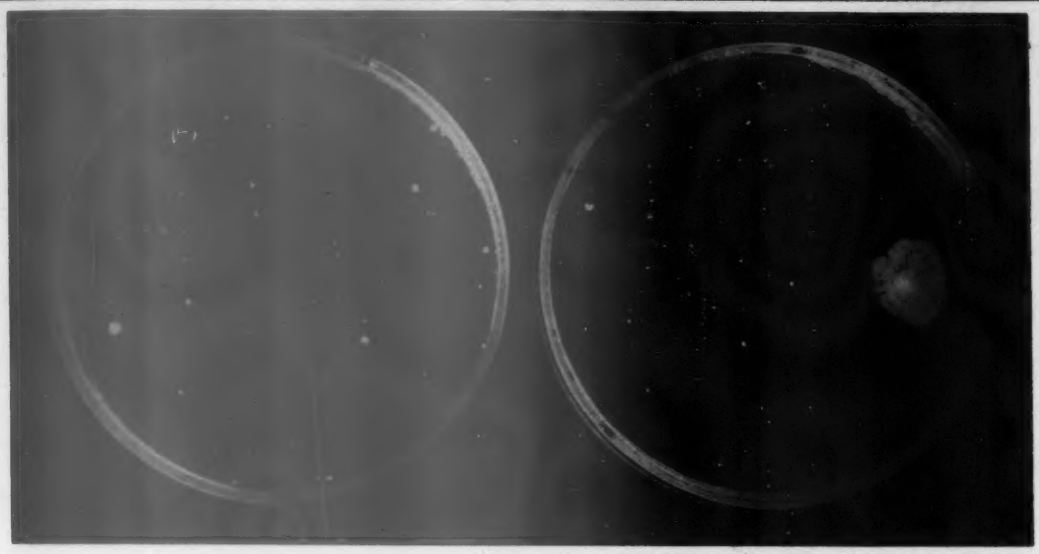


FIGURE I

(*a*) *Agar plate containing dried milk. Screened from light. Two-hundred-and-forty-seven colonies have grown.*

(*b*) *Agar plate as in* (*a*) *but exposed to light on a sunless day. Two colonies have grown.*

vegetative organisms but fails to kill the spores of the aërobic spore-forming types, which are very resistant to heat. Many of these are proteolytic rather than acid-forming, and because of the unsuitability of the *p*H produced in the reaction, are unable to compete with the lactic streptococci; they therefore cause no trouble in ordinary market milk. When, however, the milk is taken from the cows with good hygienic precautions to avoid contamination, or when the flora has been reduced by pasteurization, which does not kill spores, serious difficulty may arise from spore-formers. It was first observed at Reading, and has recently been confirmed in other laboratories, that many spores will not germinate unless some stimulus, such as, for example, the sub-lethal heat of pasteurization, is applied. Germination is then rapid, and, in the absence of competition from acid-formers, spore-forming types become predominant.

Many produce a clotting enzyme, similar to rennet, which causes the milk to gel without souring. With some types the cream on the milk, which provides the necessary highly aërobic conditions, becomes 'broken' into aggregates, possibly because the proteins adsorbed on the fat globules are disturbed by the products of bacterial metabolism. In 'sterilized' milk, in containers allowing the admission of sufficient oxygen to permit germination of the spores which have received the necessary stimulus and have survived the severe heating process, some sporing bacteria form free phenols and cresols from the tyrosine of the milk protein. Sometimes so much is formed that the milk is made unusable and the unfortunate seller is liable to be accused of fraudulent additions.

From spore-formers of several types, 'vegetable' rennets have been produced and successfully used in making cheese for communities which object to animal rennet.

The aërobic spore-formers (genus: *Bacillus*) are an interesting group but have yet to be studied intensively. They have already yielded some powerful antibiotic substances, including gramicidin. All dairy bacteriologists must have observed zones of complete inhibition of other organisms in the neighbourhood of colonies of spore-formers growing on agar plates inoculated with milk. The effect is often so marked when making agar-plate counts of dried milk as to render impossible by this method anything approaching an exact enumeration.

THERMOPHILIC BACTERIA

The members of the genus *Bacillus* grow under the most diverse conditions and are very adaptable.

FIGURE 2 – *Inhibition of growth of the tubercle bacillus. The bottles (photographed flat) contain a liquid medium inoculated on the surface with a human strain of tubercle bacillus.*
(*Left*) *Control: no added antibiotic.*
(*Centre*) *Added antibiotic: some inhibition.*
(*Right*) *Added antibiotic, greater concentration: complete inhibition (the original inoculum has not grown).*

The so-called *thermophils* may cause serious difficulty in large scale pasteurization. In this process economy in heat is achieved by using the outgoing hot milk at 63° C to warm the incoming cold milk in a heat-exchanger. The temperature is normally about 54° C, and under these conditions thermophils, both non-sporing streptococci and aërobic spore-formers, may grow rapidly. The latter may also cause serious trouble in still hotter parts of the plant. A heavy infection of organisms of this type can be eradicated only by the most meticulous cleansing with detergents, and disinfection with suitable chemical disinfectants; steam is quite ineffective. The spore-forming thermophils grow freely at temperatures far above those necessary to destroy ordinary vegetative types of bacteria. Fundamentally they are very interesting and important, since their cell contents continue to perform their vital functions under apparently impossible conditions. Their composition and general make-up must therefore differ essentially from those of ordinary bacteria. It has, indeed, been found that their 'generation time' is significantly shorter than that of other organisms. In a static culture the various phases—lag phase, logarithmic-growth phase, and the phase of decline and death—are completed in a short time. Perhaps this is an attempt of living organisms, growing at temperatures much higher than usual, to conform to van't Hoff's equation for the speed of a *chemical* reaction in relation to temperature. The phenomenon of growth at such high temperatures is all the more remarkable because the vegetative cells are killed when the temperature rises slightly above the maximum for growth. In cultures on agar plates, spore-forming thermophils from milk are abnormally sensitive to light. After passing through a plate-glass window, the Petri-dish lid, and the agar in which the organisms are embedded, weak daylight in March causes, after short exposures, a sharp reduction in the numbers which grow on subsequent incubation. Longer exposure may completely sterilize the plates. Plate cultures of dried milk (figure 1) also show that other organisms which have survived severe heating are very vulnerable to the effects of light. The exact mechanism of this reaction is not known. It may be photodynamic, through the pigment of the organism itself or of the medium, or may be due to traces of hydrogen

peroxide, to which such organisms may be expected to be more than usually sensitive.

HEAT RESISTANCE

The general question of the resistance of bacteria to destruction by heat is constantly before the milk bacteriologist. Milk as it comes from the udder of a healthy cow contains only micrococci and corynebacteria, either together or alone, in very small numbers, and these have no great heat resistance. Such milk is sterilized by pasteurization. Usually, however, milk from the udder contains a more mixed flora consisting of streptococci, staphylococci, micrococci, and corynebacteria. These, together with a small number of other organisms picked up in the course of milking, constitute the flora, numerically small, of well-produced raw milk. All of them except the corynebacteria (of a type different from those found in *aseptically* taken milk) are easily destroyed by heat. But in ordinary milk, taken from large bulks handled in the usual way, it is common to find streptococci and micrococci of which considerable numbers survive pasteurization. These organisms have acquired heat resistance during their sojourn on imperfectly cleaned and sterilized surfaces, and their resistance appears to be related to their immediate previous history. It is true that some vegetative organisms found in milk, e.g. coliform types, are able, in small numbers, to survive pasteurization, but permanent heat resistance of this type is not common and is apparently confined to a few cells in the population. There are nevertheless some vegetative organisms like the saprophytic *Microbacterium* (*Corynebacterium*), common on dirty apparatus, which can survive heating in milk to about 90° C for 10 minutes.

THE LACTIC ACID BACTERIA

Organisms of many different species cause faults in milk or dairy products, but those fermenting lactose, with lactic acid as the main end-product, are the most important for several reasons. The so-called 'lactic' streptococci, *Str. lactis* and *Str. cremoris*, are the main cause of the souring of milk at normal temperatures. They have recently been shown to belong to a distinct serological group of the genus *Streptococcus*, producing antibodies of a type which do not react with the antigens of other streptococci. They have at last been clearly differentiated from *Str. faecalis*, a common component of the flora of the gut of many animals, of which they were considered by some to be mere varieties. In milk their growth is so rapid that they usually predominate in the flora. Lactic acid is produced by the fermentation of lactose until the concentration reaches about 1 per cent. Small quantities of by-products, such as acetic and propionic acids, and acetyl-methyl-carbinol and its oxidation product diacetyl (an 'aroma' compound), are also formed. If, however, growth is slow, as at lower temperatures or in the comparatively adverse conditions of some of the milk products, the degradation of lactose to lactic acid is incomplete, and the intermediate compounds form a greater proportion of the products of fermentation. When the fermentation ceases with a lactic acid concentration of about 1 per cent., the milk attains a certain security from attack by organisms which would grow freely in it at the normal *p*H of about 6·6. In particular it is kept free from those which attack the proteins with the production of unpleasantly-tasting compounds such as peptones.

BACTERIA IN CHEESEMAKING

Without the lactic acid bacteria there would be no cheese. Cultures of lactic acid streptococci ('starter') are added to the milk and encouraged to grow rapidly by raising the temperature to about 28° C. This has the dual effect of suppressing the growth of undesirable organisms and of bringing the milk from its normal *p*H to that most favourable for the action of the clotting enzyme, rennet. Unless the physical condition of the resulting curd is thus made correct, the texture of the cheese will not be homogeneous; nor will it be sufficiently anaërobic, after moulding, to inhibit the growth of those organisms which attack the proteins. Within about three days of making, the lactose in the curd is exhausted and the growth of the streptococci ceases, although some continue to survive for long periods. Under the anaërobic conditions induced by pressure and the contraction of the curd, lactobacilli, present in small numbers in milk, begin to grow. This they do by virtue of their ability to grow at a low *p*H and in the presence of a considerable salt concentration, a property fortunately not possessed by most other bacteria. As ripening proceeds, under the influence of the rennet enzymes and the lactobacilli, the *p*H of the cheese rises from about 5 to 5·4.

If the original starter fails to produce the necessary acidity the quality of the cheese will be poor and it may be inedible. Milk usually contains small numbers of organisms of the genus

Clostridium. These are anaërobes, and the proteolytic types break down the protein molecules with the production of hydrogen sulphide and evil-smelling mercaptans. They are unable to grow in well-made cheese because of the low *p*H, but if the starter fails to produce the necessary acidity and if, by chance, the inoculum of anaërobic organisms is at all substantial, a very unpleasant mass, aptly called 'Dead Man's Finger,' will result.

BACTERIOPHAGE

Failure of the 'starter' streptococci may result from several causes. The most disastrous of these is attack by bacteriophage. Since its discovery in 1915, bacteriophage has been intensively studied, but its origin and nature are still in doubt. It appears to be a virus-like entity which penetrates the surface antigens of *actively growing* bacterial cells and brings about their disintegration and death. Bacteriophage is highly, but not absolutely, specific for bacterial types or even strains, and advantage has been taken of this property to trace the origin of, for example, staphylococci infecting a population. 'Starter' in cheese factories is usually made in bulk. If this becomes infected with phage particles which are disseminated into the air in the mist from whey separators, or which are air-borne from the cheese vats or factory sewage, the streptococci may be killed and the starter made useless for the production of acid in the milk. Alternatively, residues of whey from a vat of milk in which the phage concentration has been insufficient to prevent the development of the minimum necessary acidity may form an inoculum of such a concentration that acid development may be inhibited in milk subsequently put into the vat.

Owing to the considerable type or strain specificity, if the phage type of the starter streptococci is known, the existing culture may be replaced by another of a different phage type, and the trouble abolished. The relief is, however, likely to be only temporary, and constant vigilance is necessary. Most cultures, after attack by phage, will resume growth later, owing to the presence of certain cells which are resistant to penetration by the phage particles; but they are often, for other reasons, unsuitable as starters. It has been necessary to institute a rigid bacteriological technique in the preparation and protection of cheese starters.

ANTIBIOTIC SUBSTANCES

Bacteriophage is not the sole cause of difficulty with starter growth. If dairy utensils, e.g. milking machines, are not regularly cleansed, a flora of *Str. lactis* of a peculiar type may be established and the milk thus infected. These streptococci are themselves acid producers, but they also produce a powerful inhibitory substance and prevent the starter organisms from growing, making cheese-making difficult or impossible. As little as 3 per cent. of milk in which the inhibitory organisms have grown will prevent growth of the starter in the cheese vat. The inhibitory substance is now being investigated. It has been found to protect mice from heavy doses of virulent streptococci, and to prevent the growth of many types of streptococci of human and animal origin, *Clostridium*, *Corynebacterium*, and some species of *Bacillus*. Its most interesting property is, however, its power to inhibit *in vitro* human and bovine tubercle bacilli (figure 2). Work is proceeding here at Reading, and with colleagues in other institutions, on the isolation, purification, and testing of the substance and its therapeutic assessment. It is evidently very powerful since the best preparations inhibit the test organisms at a concentration of 6×10^{-6}.

SPARING ACTION

It was first shown here at Reading that the oxidation of vitamin C (ascorbic acid) in milk is strongly catalysed by light. It was also observed that if bacterial growth, particularly that of the harmless acid-forming types, is rapid, this oxidation is strongly opposed and under certain conditions may be prevented from proceeding. Thus it may happen that sour milk which the seller strives to avoid may contain more ascorbic acid in available form than milk with the best keeping quality! Although the quantity of ascorbic acid in average milk is comparatively small, it is a significant proportion of the average intake.

Tinned copper, because of its ease of fabrication and high heat-conductivity, has been largely used for dairy plant and apparatus, particularly milk coolers. Copper is soluble in milk, and even in small quantities acts as an oxygen catalyst and causes the rapid oxidation of the unsaturated fatty-acids of the milk, with the production of the very unpleasantly-tasting compounds in, for example, 'oily milk.' This condition is common in milk containing few bacteria and in cold weather when the growth of bacteria is slow. In warm weather, when the growth of bacteria is rapid, their reducing capacity may be sufficient to prevent the oxidation catalysed by copper. Since bare copper surfaces are potentially dangerous, they should be avoided in milk plant.

A cycle of fern anatomy

C. W. WARDLAW

It is little more than a century ago that the discovery was made that the growth of the vast majority of plants proceeds from an apical growing point. This discovery threw much light on the development of plants and was of particular value in the study of evolutionary processes. It also prepared the way for an inquiry into the causes underlying the observed forms and structures. Professor Wardlaw here gives an account, with special reference to the ferns, of the development of these two aspects of plant morphology and of the contemporary outlook.

Under the seductive influence of Goethe and the nature philosophers, botanists of the early decades of the nineteenth century were largely preoccupied with speculative problems. As working scientists their studies had largely fallen into abeyance: in many universities the science of plant anatomy and the development of microscopic technique were static or non-existent, despite the magnificent start given by the earlier exponents. This state of affairs continued until Schleiden, little more than a hundred years ago, trenchantly preached a new gospel—that the high road to discovery lay in the study of development. A period of remarkable progress ensued. Von Mohl restored the study of anatomy, while Naegeli, by addressing himself to the questions of how cells—the units of plant construction—are formed in growing vegetative organs, founded and elaborated the theory of cell formation. In particular he showed how far the processes are the same in the lower cryptogams, such as the Algae, and in vascular plants, e.g. ferns and flowering plants. It thus became possible to give a coherent account of the development of tissues and organs from the unicellular zygote, or fertilized egg, to the multicellular adult of complicated form and structure. In Naegeli's view, the history of development was not to be regarded merely as one of various ways of investigating plant form but as identical with the investigation of organic nature. He proceeded from an examination of simple organisms, such as the Algae, to the more complex types of organization seen in ferns and flowering plants. In these studies the initiation of organs and their subsequent development were referred back to cell-formation during growth at apical growing points. These observations were amplified by Wilhelm Hofmeister and others, particularly for the higher cryptogams.

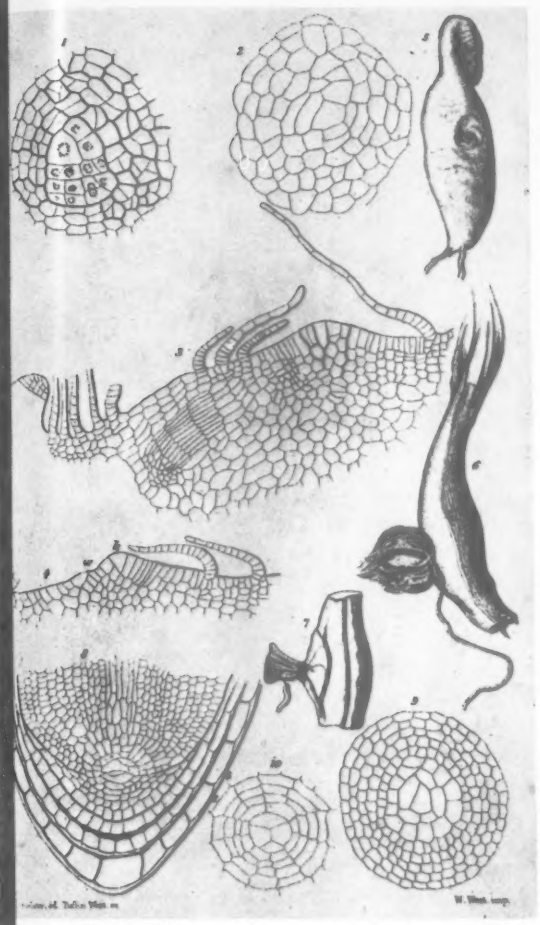
Prompted by the writings of Schleiden, Hofmeister devoted himself to a study of what was then an almost completely unexplored field, namely the reproduction and embryology of Bryophytes (mosses and liverworts) and Pteridophytes (ferns, lycopods, and horsetails), with comparable studies of seed plants. In fact, he worked out what we now describe as the 'life history' of these plants. From his cumulative experience he was able in 1851 to enunciate a generalization of the greatest importance, namely, that mosses, liverworts, the ferns and their allies, gymnosperms, and angiosperms all share a common life-cycle, characterized by the same critical events and phases in development, and by a recurrent alternation of generations. This work, enlarged and published in English in 1862 as the *Higher Cryptogamia*, is a land-mark in the development of botanical science. As an example of Hofmeister's exactitude and careful attention to detail a page of fern anatomy from the *Higher Cryptogamia* is reproduced here (figure 1). He was not without brilliant contemporaries in the same field. Of these, Stenzel deserves particular mention for his studies of the vascular anatomy of ferns, some of his reconstructions being as good as any that have ever been made (figure 2).

Although an endlessly varied and virgin field lay before him, full of treasures and surprises to delight the professed anatomist, Hofmeister's work was not merely descriptive. He was, in fact, highly endowed with the questioning, scientific mind. It was not enough for him to observe that during the development of a particular species a regular succession of characteristic changes in form and structure took place: he constantly inquired, How does the observed form come to be? To what processes of growth can the observed structural developments be related? What internal and external factors determine specific structural organization? The substance of such investigations he described in 1868 as the *General Morphology of Growing Things*. In short, he tried to apply

mechanico-physical considerations to the explanation of the development of form and structure in plants, and, together with the data of physiological experiments, to derive generalizations therefrom—an attitude which today we should consider to be truly scientific.

It might be thought that, as a result of these admirably objective inquiries, botanical science had at length been established on a broad and sure foundation, one in which morphology and physiology were seen to be inseparable aspects of the same theme. It might further be anticipated that our knowledge of the factors which influence the development of form and structure in plants would now be well advanced. But this is hardly so, and it is therefore relevant to ask the reason. The answer is to be found in another development in biology, contemporary with the causal investigations of Hofmeister. In 1859, Darwin published the *Origin of Species*. In the period that followed the enunciation of the Theory of Descent, the details of plant structure, together with such facts as could be gleaned from the fossil record, were regarded chiefly as providing materials for comparative studies and for the construction of phylogenetic systems; in everyday language, for reconstructing the 'family tree' or 'genealogical table.' There was, in brief, a very marked swing away from the causal outlook which had characterized Hofmeister's later studies. It was no longer a question of: How does the observed form come to be, in terms of nutritional, temporal, spatial, and mechanical factors? but: What family relationship, if any, is indicated by the observed form, and how can this information be applied to trace the course of evolution during descent? The general or causal morphology of Hofmeister was, in fact, displaced by the special or comparative morphology of the students of evolution. Now, it is evident that there can be no study or interpretation of evolution in plants or animals without having recourse to comparative morphology. The evidence of evolution is seen in the changing form and structure of plants during the passage of geological time, and in the diversity of form and structure in living plants. As a result of the studies which were undertaken in the phyletic interest, our knowledge of the range of plant structure was enormously extended. A vast new realm, patently worthy of exploration, must indeed have opened out before the comparative morphologist. In particular, the ferns and their allies, the progenitors of which reach back to the Upper Silurian and Early Devonian Periods, were found, more than any other class of plants, to provide the raw materials for the study of evolution. Plant anatomy, now provided with an integrating thesis of the most far-reaching possibilities and interest, had come into its own again: in particular, apical growing points, the vascular or conducting system, the spore-producing members, and the embryological development, all received close attention. In these studies, in which British botanists took a leading part, the criteria of comparison based on a study of related living organisms were checked against the evidence of the fossil record; and, bit by bit, a coherent if still speculative and necessarily incomplete account of the evolution of land plants was sketched.

Several decades passed before the methods or conclusions of the phyletic morphologists were seriously challenged. But gradually doubts began to accumulate. A bad feature of the phyletic period was that plant morphology and physiology were largely pursued as separate disciplines. Morphologists and anatomists, moreover, tended to resort to facile pseudo-physiological 'explanations' of the functions and adaptive value of tissues and organs. Such assumptions were typically not tested by experiment. Then other difficulties cropped up. Hitherto, similarity of form or structure had been tacitly accepted as an indication of genetic affinity or blood relationship, i.e. related organisms, though subject to specific and generic differences, nevertheless had the same underlying form and structure. But, as the anatomical survey was widened, it was realized that the same structural features might occur in plants which, as judged by all other criteria, were in no way related. In short, it became evident that parallel or *homoplastic* development was of frequent occurrence in the plant kingdom. This led to the view that instead of there having been one main family tree, or one main line of descent, as had generally been assumed by biologists of the Darwinian period, it was probable that there had been many parallel lines of descent from primitive ancestors. The family tree had, in fact, become a thicket. Later, the ultra-cautious and the pessimistic were to hold that it had been reduced to a bundle of sticks; that the 'genealogical table' was 'an illusory vision' and the search for common ancestors 'a hopeless quest.' Yet another consideration tended to undermine the results of comparative studies. This was a recognition of the fact that the changes in configuration undergone by an organ or tissue, e.g. the vascular system, during development, might be referable, not to



GURE 1 – *Reproduction of a plate of fern anatomy from ofmeister's* Higher Cryptogamia, 1862; *showing, for the ale Fern,* Dryopteris filix-mas: 1, 2, *downward view of the ot apex;* 3, 4, *median longitudinal sections of the shoot apex;* 6, 7, *details of lateral buds;* 8, *longitudinal section of a t tip;* 9, 10, *cross-sections of a root tip.*

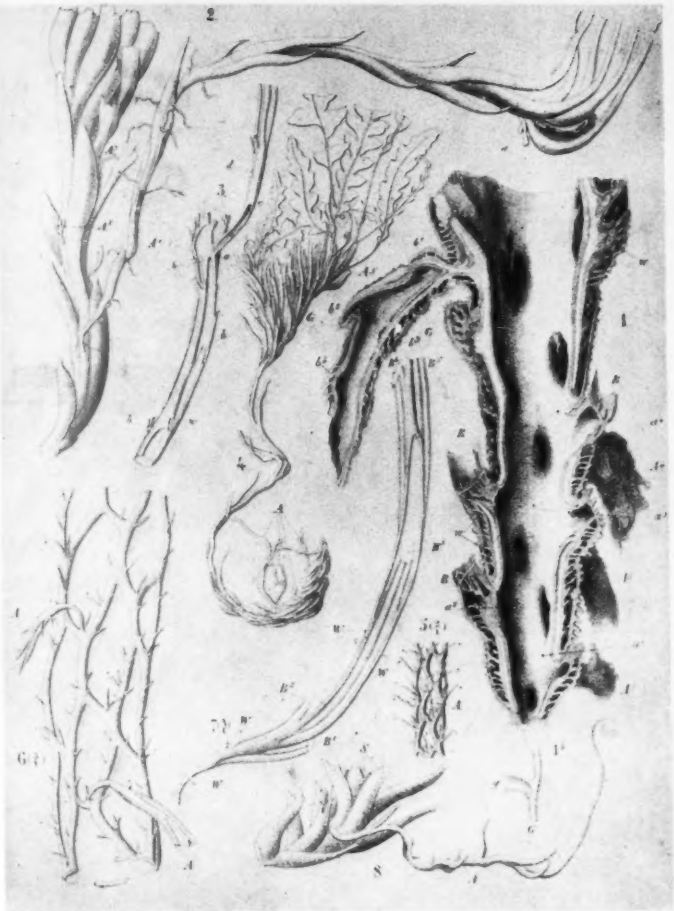


FIGURE 2 – *Reproduction of a plate of fern anatomy from a memoir by Stenzel,* 1861; *showing shoots, rhizomes, and dissections of the conducting or vascular system of a number of ferns.*

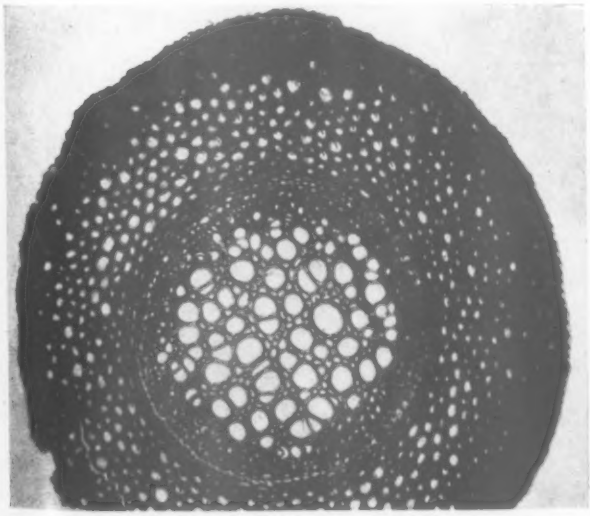


FIGURE 3 – Gleichenia dichotoma. *Transverse section of a rhizome showing the protostelic vascular system.* (× 70.)

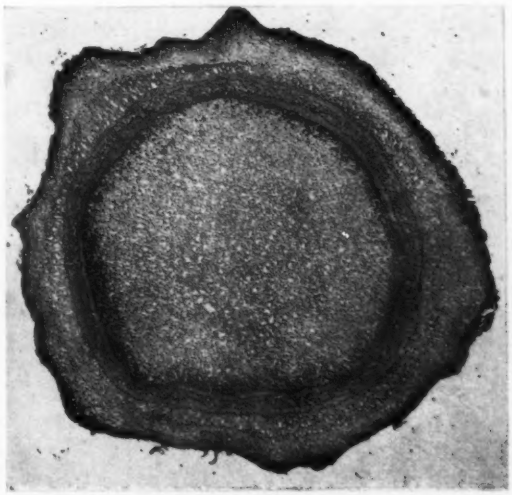


FIGURE 4 – Dryopteris aristata. *Cross-section of a shoot. The solenostelic vascular system has been induced experimentally by the systematic removal of all young leaf primordia.* (× 7.) *(Figures 3 and 4, photographs by E. Ashby.)*

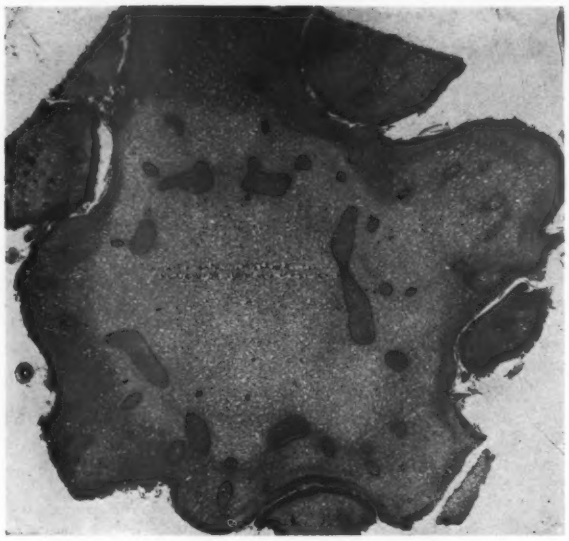


FIGURE 5 – Dryopteris aristata. *Cross-section of the same shoot as Figure 4, but lower down in the normal region, showing a dictyostelic vascular system: the separate vascular strands collectively constitute a meshwork.* (× 5.25.)

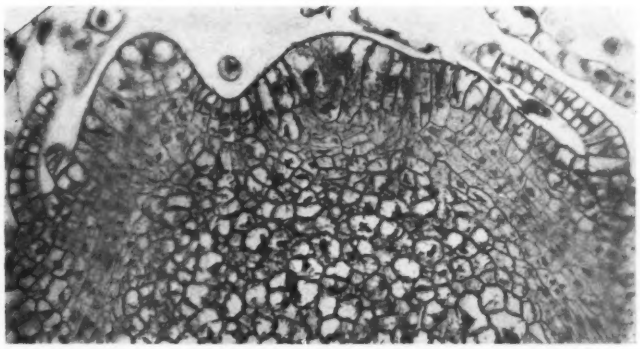


FIGURE 6 – Dryopteris aristata. *Longitudinal median section of a shoot apex, showing the apical meristem, with its conspicuous apical cell, a leaf primordium (left), scales (left and right), and the incipient vascular tissue which originates immediately below the apical meristem.* (× 126.)

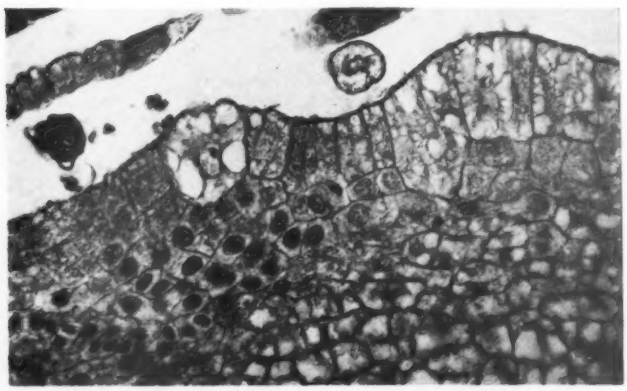


FIGURE 7 – Dryopteris aristata. *Part of the shoot apex, in longitudinal section, showing the distinctive meristematic cells. The conspicuous superficial cell (left) is the primordial cell of a leaf.* (× 240.)

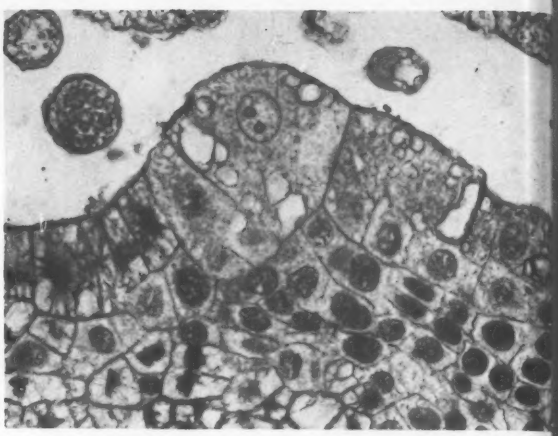


FIGURE 8 – Dryopteris aristata. *Median longitudinal sec of a leaf primordium at a very early stage of development.* (× 3

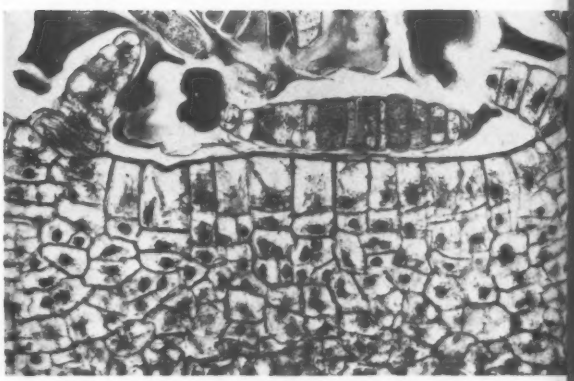


FIGURE 9 – Onoclea sensibilis. *Part of a transverse sectio a rhizome showing a bud primordium, or detached meristem, overlapping protective scales.* (× 225.)

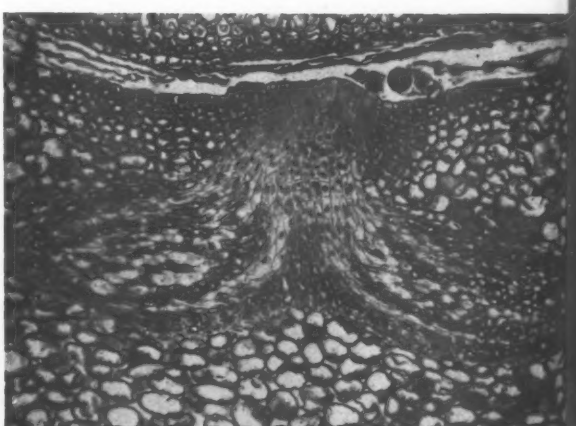


FIGURE 10 – Matteuccia struthiopteris (*The Ostrich Fe Part of a transverse section of an erect shoot showing a deta meristem developing into a lateral bud. The vascular system of bud has become confluent with two conjoined vascular strands of rhizome.* (× 90.)

(Figures 5 to 10, photographs by E. A

intrinsic factors, but to extrinsic factors such as increasing size or to the incidence of mechanical factors. In this we see a return to the Hofmeister attitude. An example may be taken from the ferns. During the phyletic period it was held that a vascular system or stele consisting of a solid core of xylem, surrounded by phloem, and known as a protostele, represented an ancient and primitive condition. Such a stele is characteristic of the earlier fossil ferns, and of living ferns regarded as primitive (figure 3); it is also present in the earlier stages of development of other ferns regarded as more advanced and derivative. Another type of stele, described as a solenostele, consisting of a cylinder of xylem with external and internal phloem and a central pith (figure 4), was regarded as being a later or derivative type. In general this type of stele occurs in ferns which are considered to occupy an intermediate position in the systematic scale. Yet a further stelar development is seen in the dictyostele (figure 5), in which the essentially cylindrical stele is perforated by wide parenchymatous leaf-gaps or meshes, so that the actual vascular tissue consists of an open meshwork. The dictyostele, which is characteristic of the most advanced modern ferns, is preceded, in individual development, by protostelic and solenostelic stages. Now, during the phyletic period, the facts of stelar morphology appeared to make a coherent and substantial thesis, namely, that stelar structure afforded one of the most useful criteria for comparative purposes, the more so as it was held that the vascular tissues were among the 'most conservative' of those to be observed in the plant. But in 1921 a new point of view was announced when Bower showed, by a wide survey of pteridophyte steles, that elaboration of form went hand in hand with an actual increase in size, physiological and mechanical factors in one way or another being causally implicated. With this observation necessarily goes the view that to the extent that structural features can be explained by causal factors, such as the size-factor, so do these features lose their value for comparative purposes and as evidence of progressive change during descent.

When one door closes, another opens. As interest in comparative studies waned, it began to be realized that, even if the phyletic history of plants were before us in full, the problems of causal morphology, i.e. the investigation of the factors relating to the assumption of form, would still remain, and that these were, as Hofmeister had so well understood, of the very essence of biological inquiry. That is, in effect, the position today: we realize that we know very little concerning the factors which influence the development of the form and structure of plants—on which data the comparative morphologists depended for their generalizations.

The past three decades have thus witnessed a marked tendency on the part of botanists to turn away from purely comparative studies to investigations of the process of development. In this study physiology has an important place. But such studies should include a consideration not only of the factors which influence the development of form and structure in the individual, but of development in its wider evolutionary sense and of the driving forces which bring it about. In the problem thus indicated, plant anatomy and experimental morphology have their place. Because of their simpler structural features the ferns, as compared with flowering plants, are regarded as affording favourable materials for investigations.

The contemporary view may be stated as follows. In vascular plants the shoot apex is the seat of all primary formative activities: all lateral appendages, leaves, scales, and buds (excepting those which are adventitious) originate at or near the apex; so, too, do all primary tissue systems. Thus, if we would understand how the external form and internal structure of any vascular plant come to be what they are, we must investigate, by all the means at our disposal, formative (or morphogenetic) processes at the apex throughout the development of the individual. Thus we return, as it were at a higher level, to a working system not greatly dissimilar to that which obtained one hundred years ago. Contemporary studies are essentially dynamic in outlook. The ferns, in particular, have proved of great value in this work, for not only do they possess a very distinct and characteristic apical meristem, with, usually, a conspicuous apical cell (figures 6, 7), but in ferns such as the Male Fern (*Dryopteris filix-mas*) or the Broad Shield Fern (*D. aristata*), the individual leaf primordium originates from a single meristematic cell (figures 7, 8). Moreover, the incipient vascular tissue can be traced to a region which immediately underlies the apical meristem, and this has given rise to the hypothesis that the initial differentiation of vascular tissue may be referred to the basipetal diffusion of a substance or substances from the active meristematic cells (figure 6).

In experimental work, buds may afford favourable materials for the investigation of developmental

processes. In the ferns, the study of the positional relationship and development of buds has yielded many points of interest. As in flowering plants, the lateral buds of ferns are inhibited by substances which proceed from the actively growing shoot apex: the destruction of the apex is usually attended by a more or less rapid growth of lateral buds. According to the proximity of the lateral bud to the apex, its vascular tissue may make a more or less complete conjunction with that of the parent shoot (figure 10) or, as in older regions, no conjunction whatsoever may be effected. As to the origin of buds, there is a question as to what relationship, if any, they bear to the apical meristem. Recent fern investigations have confirmed an earlier finding that there is a unity of origin of meristematic, i.e. formative, tissue throughout the plant: in other words, each bud primordium, consisting of superficial meristematic cells, is originally part of the apical meristem of the shoot, but becomes detached and separated during the process of growth. Such buds, or primordia, which have been described as detached meristems (figure 9), tend to occur and persist in definite positions along the shoot, and will grow into lateral shoots when the physiological dominance of the terminal meristem is removed.

In many ferns parenchymatous gaps typically occur in the shoot stele opposite the leaf-bases. The resulting characteristic dictyostele has been discussed and 'explained' in different ways, and, as we have seen, has been used in comparative studies. The relative importance of the axis or shoot and of the leaf in contributing to the vascular system has also been the subject of much discussion. For example, it has been asserted that the vascular system of the shoot is built up from the decurrent vascular strands of the leaves—that there is, in fact, no stele that is truly of axial origin. That a direct relationship exists between leaf development and the internal morphology of the shoot, and that a truly axial stele does exist in ferns, can be tested by experimental means. It has been shown that if a succession of very young leaf primordia of *Dryopteris* spp. is destroyed, the formation of the corresponding parenchymatous leaf gaps is prevented, and the vascular system of the shoot, which does in fact develop, is a solenostele, and not a dictyostele as in the normal shoot.

It has also been possible to perform a number of other experimental operations on the delicate apical region of ferns. Space does not permit of a discussion of the results which have been obtained, but, briefly, they disclose the surprising extent to which this very delicate region can be manipulated, and how varied are the morphological and structural changes that can be induced. The meristematic or formative region thus shows what has been described as considerable morphogenetic plasticity. The results of one series of experiments indicate that the idea that the vascular system of ferns is highly conservative in its nature can no longer be maintained. Nutritional, mechanical, and spatial factors are seen to be important in influencing the distribution of tissues in the growing region and therefore the ultimate pattern.

It will be evident that to the physiologist also, the growing region affords a host of problems of the greatest interest and importance. This region is, *par excellence*, the seat of formation of protoplasm and therefore of protein synthesis. From it proceed substances, such as the auxins, which exercise important effects in other parts of the plant. Thus the interest of the biochemist also becomes enlisted. For an adequate physiological investigation of the small but all-important formative region, new and refined technical methods will be required; but the data which should accrue, when integrated with those of the morphologist, will undoubtedly advance our knowledge of the process of development and render it more full and coherent. Reference should also be made to yet another aspect. The relation between genes and developmental processes has only recently begun to receive the attention which the subject so evidently deserves. At present very little is known about the actual physiological expression of a gene—how, where, and when it exerts its influence. The results in many instances, though not in all, are seen in the manifestation of characteristic formal and structural features during development. Here again it may be anticipated that the integration of the data of the two branches, genetics and morphology, will be attended by new and significant advances.

This brief account must serve as an indication of the interest and scope of experimental morphology. Clearly the results, when integrated with those of other branches of botany, should eventually have a two-fold interest. In the first place, they should provide at least partial answers to the questions propounded by Hofmeister some eighty years ago; and secondly, they should prepare the way for a critical re-examination of what must always remain one of the central and fundamental problems of biology, namely the course of descent and the process of evolution.

The metabolism of the oestrogenic hormone

G. F. MARRIAN

Recent research on the oestrogenic hormones has been marked by the increasing attention paid to the investigation of the chemical changes they undergo in the body. This investigation is a first step towards an understanding of the nature of the reactions involved when these substances produce their physiological effects. Professor Marrian here reviews our present knowledge in this field of biochemistry, and indicates lines of possible future progress.

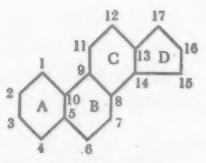
INTRODUCTION

In female animals the growth of the uterus and vagina which occurs at puberty, and the characteristic changes which occur in these accessory sex organs during 'heat' or oestrus, are produced by a physiologically active principle which is secreted by the ovary into the blood stream. If the influence of this 'oestrogenic hormone' is removed by extirpation of both ovaries, the accessory sex-organs soon become atrophic and the changes in them typical of the oestrous cycle are no longer seen. It is possible, however, to induce artificially the characteristic oestrous changes in the uterus and vagina of such an ovariectomized animal by the injection of a suitably prepared extract of ovarian tissue.

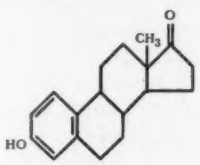
Two closely related oestrogenic substances, oestrone (I) and α-oestradiol (II), have been isolated from ovarian tissue in the chemically pure state. They possess the carbon skeleton of 1.2-*cyclo*-pentenophenanthrene and are therefore classified as steroids. As little as $\frac{1}{200000}$ mg. of α-oestradiol is sufficient when injected subcutaneously into an ovariectomized mouse to induce the typical oestrous changes in the vagina. Since oestrone is somewhat less potent than α-oestradiol in inducing vaginal oestrus in ovariectomized animals, the latter is commonly regarded as being the true oestrogenic hormone.

In man and the horse oestrogenic substances are excreted in the urine in large amounts during pregnancy, and several of these urinary oestrogens were isolated, and their structures determined, some years before the isolation of the two ovarian oestrogenic substances. The urine of pregnant women contains, in addition to oestrone and α-oestradiol, a third oestrogen, oestriol (III). The latter is present in human pregnancy urine in much larger amounts than are oestrone and α-oestradiol, but it is less potent than the two latter in inducing vaginal oestrus in ovariectomized animals.

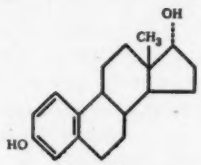
No fewer than six different oestrogenic substances have been isolated from the urine of pregnant mares. In addition to oestrone and α-oestradiol, the C_{17} stereoisomer of the latter, β-oestradiol (IV), equilin (V), equilenin (VI), and 17-dihydroequilenin (VII) have been isolated



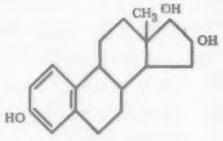
The steroid carbon skeleton



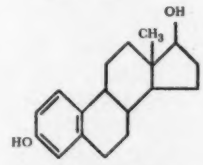
(I) *oestrone*



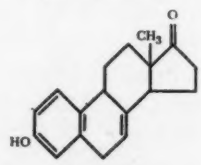
(II) *α-oestradiol*



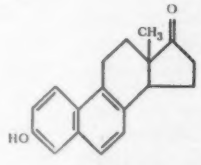
(III) *oestriol*



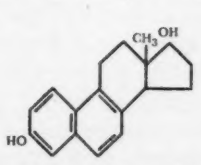
(IV) *β-oestradiol*



(V) *equilin*



(VI) *equilenin*



(VII) *17-dihydroequilenin*

from this source. It is interesting to note that oestriol has not so far been isolated from the urine of pregnant mares, while equilin, equilenin and 17-dihydroequilenin have not been isolated from the urine of pregnant women.

It is probable that the oestrogens which are excreted in such large amounts in the urine during pregnancy may be formed in the placenta rather than in the ovary. The evidence favouring this view is briefly as follows: (i) In women and in mares the amount of oestrogen excreted in the urine falls very sharply immediately after delivery; (ii) it has been observed that in women who have undergone an operation for double ovariectomy during pregnancy the level of oestrogen excretion in the urine remains high in spite of the absence of the ovaries; (iii) the same three oestrogens which occur in human pregnancy urine—oestrone, α-oestradiol, and oestriol have also been isolated from human placenta.

During recent years, research on these oestrogenic substances has entered upon a biochemical phase, in which the reactions undergone by them in the animal body have been investigated. It may be said that the ultimate object of the biochemical investigations is the elucidation of the nature of the chemical reactions involved when these substances produce their physiological effects. Although this object is still far from realization, a considerable amount of interesting information concerning the various transformations which the oestrogens may undergo in the body has been accumulated. In this article some of this recent biochemical work on the oestrogenic substances will be briefly reviewed.

CONJUGATED OESTROGENS IN URINE AND BLOOD

In the early days of the study of the urinary oestrogens it was observed independently by a number of workers that the yield of active material which could be extracted by water-immiscible organic solvents, such as ether or benzene, could be greatly increased by a preliminary boiling of the urine with acid. From these observations it was concluded that a considerable fraction of the oestrogen in both human and equine pregnancy urines was not present in the free state, but was combined in some way rendering it more soluble in water and less soluble in the water-immiscible organic solvents.

Two of the combined urinary oestrogens have so far been isolated and characterized. In 1936, Cohen and Marrian isolated an oestriol monoglucuronide from human pregnancy urine, and subsequently showed that the glucuronic acid was joined by a glucosidic linkage to either the C_{16} or C_{17} hydroxyl group of the oestriol. Schachter and Marrian (1936) showed that the oestrogens in pregnant mare's urine were mainly present as sulphuric acid esters, and subsequently (1938) they were successful in isolating from the same source the potassium salt of oestrone sulphuric acid in small yield. The work of Butenandt and Hofstetter (1939) has shown that the oestrone in human pregnancy urine is probably also present as the sulphuric acid ester. So far there is no evidence that oestriol occurs naturally as a sulphuric acid ester or that oestrone occurs as a glucuronide.

The occurrence of conjugated oestrogens is not limited to the urine. Human placenta contains a water-soluble conjugated form of oestriol (Collip *et al.*, 1934). While this conjugate has not yet been isolated as a pure substance, it seems likely that it may be an oestriol monoglucuronide identical with that present in human pregnancy urine. Mühlbock (1937, 1939) showed that the amount of oestrogen extractable by water-immiscible fat solvents from the blood of pregnant mares and of pregnant women could be increased by a preliminary boiling with acid. The presence of water-soluble conjugated oestrogen in the blood of pregnant women has been recently confirmed by Rakoff *et al.* (1943). These authors have put forward evidence, which does not appear to be entirely conclusive, that the blood oestrogen may be bound to the serum proteins. Since the conjugated oestrogen in blood is clearly the 'transport' form of the hormone its isolation in a state of chemical purity and its characterization would obviously be most desirable.

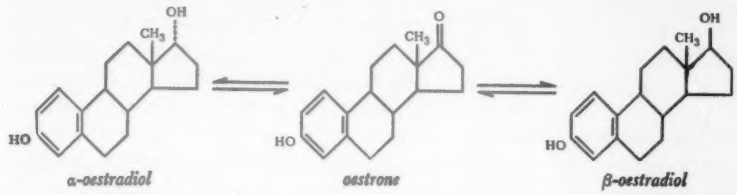
THE INTERCONVERSION OF OESTRONE AND THE OESTRADIOLS IN THE ANIMAL BODY

The occurrence of the two stereoisomeric oestradiols together with oestrone in the urine of pregnant mares suggests that the former may both be formed from oestrone by the reduction of the ketonic group. There is, indeed, direct evidence that such a reduction actually occurs in the animal body. Stroud (1939) has isolated β-oestradiol from the urine of rabbits after the administration of oestrone, while Pearlman and Pincus (1942) have detected the presence of α-oestradiol in the urine of men following oestrone administration.

The experiments of Heard and his co-workers (1941) have provided evidence not only for the reduction of oestrone in the body, but for the

oxidation of oestradiol to oestrone. Following the administration of α-oestradiol to rabbits and to a man they were able to isolate both oestrone and β-oestradiol from the urine in the first case and oestrone alone in the second. Heard's findings with rabbits have been confirmed by Fish and Dorfman (1942).

There are therefore good grounds for believing that the two oestradiols and oestrone are to some extent interconvertible in the animal body, as shown in the following scheme:



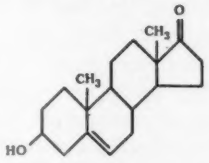
α-oestradiol *oestrone* *β-oestradiol*

THE CONVERSION OF OESTRONE TO OESTRIOL

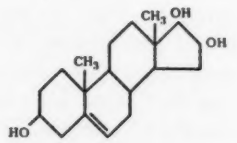
In 1937, Pincus and Zahl claimed to have demonstrated the excretion of oestriol in the urine of rabbits following the administration of oestrone. In these experiments, however, the presence of oestriol was inferred from a colour reaction and was not confirmed by isolation and characterization of the pure substance. More recently Heard and his co-workers (1941), and Fish and Dorfman (1942), have failed to isolate oestriol from the urine of rabbits and guinea pigs after the administration of oestrone.

There is, however, good evidence that in man oestrone may be converted into oestriol. Following the administration of a large amount of oestrone to a young man, Pearlman and Pincus (1942) have isolated oestriol from the urine in a small yield and have satisfactorily characterized it. It does not necessarily follow from this, however, that the oestriol found in the urine of pregnant women is formed in the body from oestrone or α-oestradiol and is merely an end-product of the metabolism of these oestrogens. It is at least possible that oestriol may be directly synthesized in the human placenta, and that it may have some specific but so far unknown functions during pregnancy.

It seems possible that other 17-ketosteroids besides oestrone may be transformed in the body to steroids with hydroxyl groups at positions 16 and 17. Hirschmann (1943) has recently isolated from the urine of a boy with a tumour of the adrenal glands a steroid belonging to the male hormone series which has hydroxyl groups at positions 3, 16, and 17. It is an attractive hypothesis that this Δ^5-androstene-3, 16, 17-triol may bear the same structural and biological relationship to dehydroisoandrosterone[1] as does oestriol to oestrone. However, until it has been shown that the steric configurations of the C_{16} and C_{17} hydroxyl groups are the same in this androstenetriol and in oestriol, and until it has been definitely proved that the former compound can be produced in the body from dehydroisoandrosterone, this hypothesis must be viewed with some caution. It has been shown recently by Marrian and Butler (1944) that the same androstenetriol is present in small amounts in the urines of normal men and women. It is evident therefore that the metabolic path by which it is formed in the body is a normal one.



Dehydroisoandrosterone



Δ^5-androstene-3 (α), 16, 17-triol

DEHYDROGENATIONS AND HYDROGENATIONS IN THE OESTROGEN CARBON SKELETON

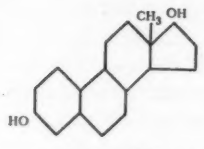
Evidence of a rather inconclusive nature is accumulating which indicates that dehydrogenations and hydrogenations of the oestrogen ring system may occur in the body, in addition to the oxidations and reductions of the substituent groups which have been discussed above.

In the mare, as pregnancy advances, the amounts of equilin and equilenin, relative to the amount of oestrone, increase. On the basis of these facts it has been suggested that equilin and equilenin may be formed in the mare by successive partial dehydrogenations of oestrone. This suggestion is not one that can be easily tested by direct experimentation, as will be readily understood.

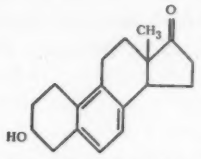
The possibility that the aromatic ring in oestrone may undergo complete hydrogenation in the

[1] Dehydroisoandrosterone is a steroid possessing androgenic activity which is found in the urine of both men and women. Since the amounts of this steroid excreted in the urine are greatly increased in certain cases of cancer or enlargement of the adrenal glands, and since it is still excreted after removal of the testes or ovaries, it is generally believed that it originates in the adrenal glands.

body was raised by the isolation by Marker *et al.* (1938) of two isomeric oestranediols from the urine of non-pregnant women. These oestrogen reduction products were not found in the urine of pregnant women, and accordingly Marker *et al.* suggested that their formation may be associated with the normal utilization of the hormone in the menstrual cycle.



oestranediol



$\Delta^{5,7,9}$-oestratriene-3-ol-17-one

Further indirect evidence favouring the view that ring A in the oestrogen molecule may undergo complete hydrogenation in the body was obtained when Heard and Hoffman (1940, 1941) isolated *$\Delta^{5,7,9}$-oestratriene-3-ol-17-one*, a bond isomer of oestrone in which ring B instead of ring A is aromatic, from the urine of pregnant mares. Since it has been shown by Ruzicka *et al.* (1938) and by David (1938) that *$\Delta^{5,7,9}$-oestratriene-3, 17-diol* can be formed from equilenin by reduction with sodium and ethanol, Heard and Hoffman suggest that *$\Delta^{5,7,9}$-oestratriene-3-ol-17-one* may be formed in the body from equilenin by an analogous preferential hydrogenation of ring A.

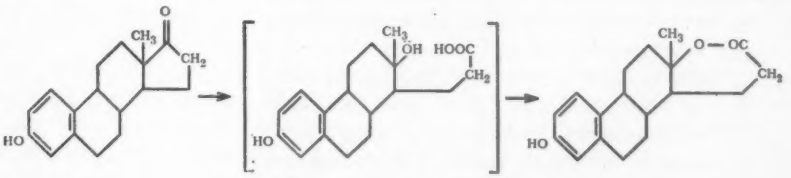
OESTROGEN INACTIVATION IN THE ANIMAL BODY

It has been demonstrated by a number of different workers that only a small fraction of the activity of oestrogen administered to animals can be satisfactorily recovered from the excreta and the carcase. It is evident therefore that the animal body possesses considerable powers of inactivating administered oestrogens, and it is therefore reasonable to assume that much of the endogenous oestrogen is similarly inactivated.

A considerable amount of evidence has been accumulated which indicates that the liver may be the principal site of oestrogen inactivation in the body. Thus Zondek (1934) showed that oestrogen was inactivated *in vitro* in the presence of liver mash but not in the presence of the mash of other organs, while more recently Heller *et al.* (1939) have shown that oestrogens are inactivated by slices of rat liver but not by slices of rat lung, spleen, or uterus. Israel *et al.* (1937) found that oestrogen perfused through a heart-lung preparation was inactivated when the liver was in the circuit, but was not inactivated in the absence of the liver.

It is believed by some that oestrogen inactivation in the liver may be the result of an enzymic oxidation process, although the enzymic system responsible has not yet been characterized, nor has any physiologically inactive oxidation product of an oestrogen been isolated so far from animal tissues or excreta. In this connection, however, the work of Westerfeld (1942) is of considerable interest. On treatment of oestrone in alkaline solution with hydrogen peroxide at room temperature for several days, he obtained as the main product the lactone of an acid formed by the rupture of ring D between carbon atoms 13 and 17. Since the course of oxidation of many substances in the animal body can be imitated in the laboratory by oxidation with hydrogen peroxide it is possible that the inactivation products of oestrogen in the body may be substances of this type, although Heard and Hoffman (1941) failed to isolate any such compound from the urine of a man after the administration of large amounts of oestrogen.

Recent work by O. W. Smith (1944) suggests that oestrogen oxidation products of the type of Westerfeld's lactone, if they are actually formed in the body, may be of considerable physiological importance. It has been known for many years that the administration of oestrogens to animals stimulates the activity and increases the size of the anterior lobe of the pituitary gland, secondary results of this stimulation being a partial exhaustion of the gonadotrophic activity of the gland and an increase in the size of the adrenal glands owing to increased production of the pituitary adrenotrophic factor. As a result of the very extensive observations made by himself and his co-workers on oestrogen excretion in women, Smith developed the theory that certain of the physiological effects generally ascribed to the oestrogens, and in



Oxidation of oestrone by hydrogen peroxide

particular the effect on the arterior pituitary gland, might be due to oestrogen degradation products formed in the body rather than to the oestrogens themselves. Smith was therefore led to investigate the pituitary-stimulating action of Westerfeld's lactone. It was found that this compound, which possesses only a small fraction of the oestrogenic activity of oestrone when tested by the usual method involving the production of the characteristic oestrous changes in the vaginae of ovariectomized animals, was considerably more potent than oestrone in its effect on the anterior pituitary body. This extremely important finding suggests the possibility that the physiological significance of oestrogen inactivation in the body may be much greater than has been hitherto supposed, and it should undoubtedly stimulate a more thorough investigation of the chemical nature of the inactivation process.

Campbell and Hey (1944) have recently pointed out that the oestrogen content of different urines (human, mare's, and stallion's) is roughly proportional to their content of *p*-cresol. They therefore suggest that tyrosine may not be the only source of the urinary *p*-cresol as is usually supposed, and that some of the latter may be derived from the degradation of oestrogens and other steroids in the body. It is to be hoped that this interesting suggestion will be followed up by a direct experimental attack.

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Book reviews

AN EXPERIMENTAL COURSE IN OPTICS

Practical Optics, *by B. K. Johnson. Pp. viii + 189. The Hatton Press Limited, London.* 1945. 15*s. net.*

When an author has a wealth of experience both of teaching and of practising his subject, it is inevitable—given moderate fluency—that he should produce a competent work. These are, in fact, the qualities which B. K. Johnson has brought to bear on the writing of *Practical Optics*.

The experiments of the earlier chapters, which illustrate the paths taken by the image-forming light through optical components and systems, should very soon find a place in elementary courses on light.

In Chapter III the principles of the telescope are dealt with in adequate detail. It is a pity that the treatment is marred by a seriously misleading representation of the 'star-test' appearances of aberrated and aberration-free objectives. The reader would be well advised to consult the photographs in H. D. Taylor's *Testing and Adjustment of Telescopic Objectives*.

In dealing with the microscope, resolution is calculated assuming non-coherent star objects instead of a periodic structure with phase-related illumination. This latter leads to Abbe's formula, which is the one usually given. The section on ultra-violet microscopy is one where the author can (and does) speak with undeniable authority. In contrast, the developments in photographic lenses of the last twenty or thirty years are completely, and unjustifiably, ignored.

There are two typographical errors: in the spelling of *Amphipleura* (p. 83), and in fig. 127, which reads Coolne instead of Cooke. These will no doubt be corrected in a second edition, which this book deserves, and which it should get.

H. H. HOPKINS

INTERPRETATION OF PERIODIC WAVES

Wave-form Analysis, *by R. G. Manby. Pp. xi + 275. Chapman & Hall Limited, London.* 1945. 21*s. net.*

Mr Manby has written this book as a result of his experience in the Vibration Department of the de Havilland Aircraft Company. The book might appropriately be renamed, 'What every young engineer should know about Fourier Series.' The young engineer should know a considerable amount. The book contains mathematical chapters discussing Fourier's theorem itself, and giving the expansion of many functions of different types. The greater part of the book, however, deals with the practical technique of wave-form analysis as practised in an engineering concern. From, for instance, a strain gauge record, it was required to estimate as accurately as practicable the amplitudes and frequencies of the principal constituents of the waves. When the author first undertook this work, he found that very little published information was available about the technique for doing this. He therefore developed his own technique, and this book was the result. It should be invaluable to anyone faced with a similar task. Besides the purely mathematical chapters, the practical methods of analysis are discussed in detail, including mechanical aids. There are also numerous illustrations of vibration records obtained in practice. One chapter is devoted to Lissajou figures.

N. F. MOTT

ANALYSIS OF ORGANIC COMPOUNDS

Organic Reagents for Organic Analysis, *by the Staff of the Research Laboratory of Hopkin & Williams Limited. Pp.* 172. *Hopkin & Williams Limited, London.* 1944. 5*s.* 6*d. net.*

This small volume lists the most important reagents for the following: carboxylic acids; alcohols; aldehydes and ketones; alkaloids; amides; primary, secondary, and tertiary amines; barbituric derivatives; ethers; halides; aromatic hydrocarbons; mercaptans; nitriles; phenols; sulphonamides; and sulphonic acids. Selected references to the original literature are included. In accordance with the authors' aim—'the use of organic reagents in preparing derivatives of organic substances for purposes of identification by melting points'—the various substances are divided into 'selected reagents' and 'other reagents,' and experimental details and melting points are given only for the former. The choice is governed largely by the accessibility and stability of the reagent, by the ease with which derivatives can be prepared and purified, and by the diversity of melting points for closely related compounds. In checking some of the published melting points, the authors have found 'a surprisingly large number of cases where the literature and reference books are contradictory and inaccurate.' Tables of melting points of the various derivatives of the 'selected reagents' are given at the end of the book.

All who are interested in qualitative organic analysis will find this book useful and will doubtless wish to possess a copy. Its utility would be increased by the provision (*a*) of more experimental details where these are not given in the text, and (*b*) of alternative experimental methods (where available) in applying some of the reagents. The book is well produced; there is a good index.

A. I. VOGEL

STRUCTURE OF INORGANIC COMPOUNDS

Structural Inorganic Chemistry, *by A. F. Wells. Pp. viii* + 590. *Clarendon Press, Oxford.* 1945. 25*s. net.*

We owe the first seeds of structural inorganic chemistry to the early work of the Braggs a quarter of a century ago, when they applied X-ray analysis to rock-salt and other cubic crystals. After some years of slow but steady development the subject branched out astonishingly in many directions and its growth became almost rank. As a result of this accurate new information the structures of many substances such as bleaching powder, lead oxides, phosphorus pentachloride, and the silicates have been shown to be very different from those deduced by earlier chemistry. Many new problems have appeared and have been answered, especially relating to metals, with an enormous widening of the chemist's understanding of the properties of atoms and molecules.

This book gives a very comprehensive account of the results of the above work in inorganic chemistry. The author, though now a crystallographer, has the great advantage of having originally been a chemist, and the book is written as from one chemist to another. The author will earn the gratitude of many for his very clear treatment of each aspect of the subject. The length of the book presents a problem to the unfortunate student. The subject is, however, so various and ramifying, and impinges on ordinary chemistry in so many ways, that almost any mode of arrangement is bound to be hard-going for the newcomer.

E. J. BOWEN

CURRENT METHODS OF COLORIMETRIC ANALYSIS

Colorimetric Analysis, *by Noel L. Allport. Pp. xii* + 452, *with* 37 *tables. Chapman & Hall Limited, London.* 1945. 32*s.* net.

The determination of substances present in very low concentrations and the analysis of very small samples are problems of increasing importance in chemical research. The particular suitability of colorimetry for analyses of this kind, and its convenience in routine analysis where great accuracy is unnecessary, make Mr. Allport's comprehensive account of current methods a valuable addition to chemical literature.

This book is essentially one for the laboratory worker, since theoretical discussions have been deliberately reduced to a minimum. This omission is, however, balanced by comprehensive literature references. The text is divided into a series of monographs devoted to methods used for the determination of specific substances or radicals. The general introduction to each is followed by full practical details of those methods which have been proved reliable after adequate trial. Each method is critically discussed and its limitations are described. Modifications necessary for the analysis of particular materials, such as foodstuffs, are given.

The text is well planned and the over-lapping of subjects largely avoided. The critical approach and frequent references to personal experience stamp the author as a master of his subject. Unlike many enthusiasts, however, he avoids the error of claiming for the methods greater accuracy than they can attain in ordinary practice. This caution is very necessary in discussing colorimetric methods, because of their particular susceptibility to interference by extraneous substances.

Mr. Allport is to be congratulated on a book which is both well written and technically sound and up-to-date. All research workers who use colorimetry will find it a most valuable book of reference.

Notes on contributors

JULIAN S. HUXLEY,
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Is eminent both as a biologist and as a writer. He was born in 1887 and was educated at Eton and Balliol College, Oxford, where he had a brilliant academic career. He was Newdigate Prizeman in 1908 and obtained first-class honours in zoology in the following year. He was elected to a Naples Scholarship in 1909. From 1910–12 he was Lecturer in Zoology at Balliol. From 1912–16 he was at the Rice Institution, Houston, Texas, first as Research Associate and later as Assistant Professor. In 1919 he returned to Oxford as Fellow of New College and Senior Demonstrator in Zoology. From 1925–27 he was Professor of Zoology at King's College, London; during part of this time (1926–29) he was also Fullerian Professor of Physiology at the Royal Institution. In 1935 he was appointed secretary of the Zoological Society of London, an office he held until 1942. The many other offices he has filled include that of President of the Institute of Animal Behaviour, Vice-president of the Eugenics Society, and Chairman of the Association for the Study of Systematics. From 1926–29 he was President of the National Union of Scientific Workers. He is also the author of many books and papers on biological, philosophical, and political subjects, and is keenly interested in the making of biological films.

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Since 1935 has been Bishop of Truro, where he was born in 1887. He was educated at the Leys School, Cambridge, and at Gonville and Caius College, Cambridge. His university career was specially distinguished, for he was not only classed as a wrangler in the mathematical tripos, but obtained first-class honours in theology. For some years after the war of 1914–18 he was Dean and Tutor of his college, Senior Proctor, and Secretary of the General Board of Studies. A well-known author, he has written many books and papers on theology. He is an accomplished field botanist, and turns his botanical knowledge to practical account in his hobby of gardening.

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Was born in 1879 and was educated at Mill Hill School and Faraday House, London. He joined the staff of the National Physical Laboratory in its very early days; his first work there was to establish a National Unit of Candle Power. Problems connected with light and lighting have since been his main interest. In 1918 he was appointed the first Director of the Research Laboratories at Wembley of the General Electric Company, a position he still holds. He is a past president of the Institution of Electrical Engineers, of the Institute of Physics, and of the Illuminating Engineers' Society. During the recent war he led a research team in the investigation of radiolocation.

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Was born in 1901 and was educated at Paisley Grammar School and Glasgow University. From 1921–28 he was lecturer in Botany and Mycology at Glasgow. In 1928 he joined the staff of the Imperial College of Tropical Agriculture, Trinidad, British West Indies, to investigate problems relating to diseases of the banana and the transport and storage of tropical fruit. In connection with his work he travelled widely in Central and South America; and through his contacts with planters, shippers, and distributors he has become a recognized authority on these subjects. He has long held the view that tropical botany ought to be given the fullest support, not only for utilitarian reasons but for the possibilities it affords of advancing the science as a whole. Since 1940 he has been Professor of Cryptogamic Botany in the University of Manchester.

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Was born in 1904 and was educated at Tollington School and University College, London. He has had a distinguished and varied academic career. In the University of London he has been successively Beit Memorial Fellow for Medical Research (1927–30) and Lecturer in Biochemistry (1930–33). In 1931 he was awarded the Meldola Medal of the Institute (now the Royal Institute) of Chemistry. In 1933 he was appointed Associate Professor of Biochemistry at Toronto, acceding to the full Professorship in 1936. Since 1939 he has been Professor of Chemistry in Relation to Medicine in the University of Edinburgh. He is the author of many papers on biochemistry; in this field his main interest is in the chemistry of the sex-hormones.

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